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Reports
Fule,
P. Z.

Fire in the Urban/Wildland interface



SCHOOL OF FORESTRY

March 31, 2004

Dr. Carl Edminster, Project Leader
Rocky Mountain Research Station
2500 S. Pine Knoll Drive
Flagstaff, Arizona 86001

Dear Carl,

TITLE:

I am pleased to enclose the final report for RMRS-99158-RJVA, "Fire in the urban/wildland interface." I apologize for the delay in completing this research. As we have discussed previously, our sampling time was greatly extended due to the droughts and forest closures in 2000 and 2002, as well as the Leroux Fire in the study area in 2001. As a result, we were only able to complete forest sampling in 2003.

On the following page, I have given you a list of the presentations, publications, and manuscripts supported in full or in part by this research. I have also attached copies of the publications.

I would like to thank you, the Rocky Mountain Research Station, and the Coconino National Forest for supporting the research.

Sincerely yours,

Pete Fulé

Presentations

- Crouse, J.E., M.M. Moore, and P.Z. Fulé. 2000. Forty years of land use/land cover change in the urban-wildland interface, Flagstaff, Arizona. April 4-6, 2000, RS-2000 USDA Forest Service Remote Sensing Conference, Albuquerque, NM.
- Fisher, M., P.Z. Fulé, and N.C. Johnson. 2003. Competition between native grasses in the presence of arbuscular mycorrhizal communities from different elevations. Seventh Biennial Conference of Research on the Colorado Plateau, Flagstaff, AZ, November 5, 2003.
- Cocke, A.E., M.A. Fisher, J.E. Crouse, and P.Z. Fulé. 2003. Multiple studies on an elevational gradient, San Francisco Peaks. Southwest Fire Initiative Conference, Flagstaff, AZ, April 29, 2003.
- Fisher, M., A. Cocke, J. Crouse, and P.Z. Fulé. Vegetation Gradients on the San Francisco Peaks. M. Fisher, A. Cocke, J. Crouse, and P.Z. Fulé. 2003. NAU Environmental Research on National Forests and Adjacent Lands Meeting, February 3, 2003.

Theses

- Cocke, A. (2004). Fire exclusion and burn severity on the San Francisco Peaks, Arizona. M.S. Thesis, School of Forestry, Northern Arizona University, Flagstaff.
- Fisher, M. (2004). Plant and plant-mycorrhizal interactions across an elevation gradient on the San Francisco Peaks. M.S. Thesis, School of Forestry, Northern Arizona University, Flagstaff.

Peer-reviewed Publications (in review and in preparation)

- Cocke, A.E., P.Z. Fulé, and J.E. Crouse. In review. Assessment of burn severity using Landsat 7 ETM+ imagery and ground data. International Journal of Wildland Fire.
- Fisher, M., P.Z. Fulé, and N. Johnson. In prep. Changes in forest vegetation and arbuscular mycorrhizae along a steep elevation gradient in Arizona. To be submitted to Forest Ecology and Management.

Other Publications

- Fulé, P.Z., C. McHugh, T.A. Heinlein, and W.W. Covington. 2001. Potential fire behavior is reduced following forest restoration treatments (peer-reviewed). Pages 28-35 in Vance, G.K., C.B. Edminster, W.W. Covington, and J.A. Blake (compilers), Ponderosa Pine Ecosystems Restoration and Conservation: Steps Toward Stewardship. Proc. RMRS-P-22. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Crouse, J.E., and P.Z. Fulé. 2003. Species and canopy cover map development using Landsat 7 Enhanced Thematic Mapper Imagery for Grand Canyon National Park. Proceedings: Ninth Forest Service Remote Sensing Applications Conference. USDA Forest Service/American Society for Photogrammetry and Remote Sensing (electronic publication).

FINAL REPORT—MARCH 31, 2004

Fire in the Urban/Wildland Interface: A Landscape Modeling Approach

Research Joint Venture Agreement No. RMRS-99158-RJVA

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Table of Contents

Executive Summary.....	2
Chapter 1: Overview of Accomplishments.....	4
Chapter 2: Forest Change on the San Francisco Peaks, Arizona	5
Chapter 3: Changes in Forest Vegetation and Arbuscular Mycorrhizae Along a Steep Elevational Gradient in Arizona	35
APPENDIX 1: PLOT LAYOUT	66
APPENDIX 2: CONSOLIDATION OF SPECIES	67
APPENDIX 3: COMPLETE SPECIES LIST.....	70

Executive Summary

The project “Fire in the Urban/Wildland Interface: A Landscape Modeling Approach” was designed as an integrated landscape modeling approach to support the goals of forest restoration projects advanced by the Greater Flagstaff Forests Partnership and Coconino National Forest: restoring natural ecosystem functions, reducing catastrophic fire risk, and researching the implications of these efforts. We measured forest conditions on treatment sites and adjacent high-elevation slopes that the restoration projects were intended to protect. We modeled changes in forest structure associated with fire exclusion and with restoration treatments, as well as fire behavior implications of treatment.

Fire Behavior Implications of Alternative Treatments: Potential fire behavior was compared under severe weather conditions in 12 ponderosa pine stands treated with alternative thinning prescriptions in the wildland/urban interface of Flagstaff, Arizona. Prior to thinning, stands averaged 474 trees/acre, 158 ft²/acre basal area, crown bulk density 0.0045 lb/ft³, and crown base height 19.2 ft. Three thinning treatments differing in residual tree density were applied to each of 3 stands (total of 9 treated, 3 control). Treatments were based on historic forest structure prior to Euro-American settlement and disruption of the frequent fire regime (*circa* 1876). Thinning reduced stand densities 77-88%, basal areas 35-66%, crown bulk densities 24-48%, and raised crown base height an average of 11 ft. Before thinning, simulated fire behavior under the 97th percentile of June fire weather conditions was predicted to be intense but controllable (5.4 ft flame lengths). However, active or passive crownfires were simulated using crown base heights in the lowest quintile (20%) or winds gusting to 30 mph, representing the fuel ladders and wind gusts that are important for initiating crown burning. Under the identical conditions after thinning, all three treatments resisted crown burning. The degree of resistance was related to thinning intensity. It is crucial to remove thinning slash fuels through prescribed burning or other means. If not removed, slash fuels can cause crownfire behavior in the thinned stands under severe wildfire conditions. Finally, the crownfire resistance achieved through thinning will deteriorate over time unless maintenance burning and/or thinning is continued.

Forest Structure: The San Francisco Peaks, the tallest mountains in Arizona, create a steep elevational gradient supporting five distinct forest types: ponderosa pine, mixed conifer, aspen, Englemann spruce-subalpine fir, and bristlecone pine. Fire has been excluded since circa 1880 (last fires in 1876 and 1879). We examined how changes in structure and composition since fire exclusion have varied by forest types, contrasting the results with similar forest types on a gradual elevation gradient at the Grand Canyon. Except for the lowest elevation forests, the Peaks have not been harvested for timber and are currently managed as a Wilderness area, so management impacts have been relatively limited. One hundred thirty-five plots were measured from 2442 to 3559 meters elevation on the south side of the San Francisco Peaks. Using dendrochronological data and modeling, forest structure was reconstructed for 1876. Contemporary forest density was greatest in Spruce-fir (840 trees/ha) and least in Bristlecone (546 trees/ha). Basal area ranged from 57.8 m²/ha for Spruce-fir to 34.4 m²/ha for Ponderosa pine. Litter depths ranged from an average of 0.73 cm in the Bristlecone pine forest type to 1.62 cm in the Ponderosa pine forest type. Duff depth was lowest in Bristlecone forests (1.79 cm), but was highest in Spruce-fir forests (4.32 cm). Total woody debris ranged from 62.0-132.2 Mg/ha. Greatest regeneration occurred in the Aspen forest type but virtually no aspen sprouts survived to sapling size. All forest types had lower densities and basal areas in 1876 than in 2000. Density increases were greatest in Ponderosa pine (1073%) and least in Bristlecone pine (92%). However, changes in basal area were greatest in Aspen stands (456%) and lowest in Bristlecone pine stands (69%). In low- to

mid-elevation forests, invasion of shade-tolerant conifers has altered forest composition. Aspen stands may also be declining on the Peaks. Because changes were least in high elevation forests, these areas may be less impacted by fire exclusion. Nonetheless, higher elevation forests remain at risk of change due to potential global warming. Fire exclusion has caused species to migrate into lower elevation creating less resilience to increased temperatures. Biodiversity, fire and other disturbance patterns, and susceptibility to pathogens have already been altered due to fire exclusion and may lead to increased probability of further unusually rapid changes under climate conditions projected for the near future.

Plant Community and Mycorrhizal Relationships: The San Francisco Peaks have a high conservation value both because of their importance to the human population and the locally rare habitat found there. However, vegetation studies have chiefly been limited to species lists. In this study we assessed species composition, richness and abundance of understory vegetation, as well as arbuscular mycorrhizal inoculum potential on the San Francisco Peaks, crossing a steep, south-facing elevational gradient. Because coniferous trees do not form associations with arbuscular mycorrhizal fungi, there may be more variation in coniferous forest than in ecosystems where all species associate with arbuscular mycorrhizal fungi. Differences in species composition between forest types reflected differences in the historical disturbance regimes. Species richness was highest in ponderosa pine forest (32.6 ± 1.4 per 1000 m² plot), although plant abundance was highest in aspen forest ($49.4\% \pm 3.8$). Ponderosa pine and bristlecone pine forest were both high in species richness and contained species which were tolerant of frequent low intensity fire. Exotic species richness and abundance were highest in the lower elevations, which were also areas of high species richness and greater anthropogenic disturbance. Arbuscular mycorrhizal inoculum potential varied between (1.2% and 80.1%), decreasing with increases in tree cover. We suggest indicator species that may be of use in monitoring these forests under changing climate and fire regimes.

Chapter 1: Overview of Accomplishments

The project had five components. Below we have listed the research accomplishments, including citations for published work.

- 1) Creating the landscape: The San Francisco Peaks landscape was developed using remotely sensed imagery with the methodology described in: Crouse, J.E., and P.Z. Fulé. 2003. Species and canopy cover map development using Landsat 7 Enhanced Thematic Mapper Imagery for Grand Canyon National Park. Proceedings: Ninth Forest Service Remote Sensing Applications Conference. USDA Forest Service/American Society for Photogrammetry and Remote Sensing (electronic publication). This publication is attached.
- 2) Changes in the interface: Changes in the interface were described in: Crouse, J.E., M.M. Moore, and P.Z. Fulé. 2000. Forty years of land use/land cover change in the urban-wildland interface, Flagstaff, Arizona. April 4-6, 2000, RS-2000 USDA Forest Service Remote Sensing Conference, Albuquerque, NM.
- 3) Changes in the forest: Chapters 2 and 3 of this report.
- 4) Testing alternatives: Fire behavior implications of alternative forest management approaches are described in: Fulé, P.Z., C. McHugh, T.A. Heinlein, and W.W. Covington. 2001. Potential fire behavior is reduced following forest restoration treatments (peer-reviewed). Pages 28-35 in Vance, G.K., C.B. Edminster, W.W. Covington, and J.A. Blake (compilers), Ponderosa Pine Ecosystems Restoration and Conservation: Steps Toward Stewardship. Proc. RMRS-P-22. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. This publication is attached.
- 5) Subsequent Phases: Due to delays in field sampling and ending of funding with phase two (2000), subsequent work was not undertaken. However, related work was done with outside funding, as described in: Cocke, A.E, P.Z. Fulé, and J.E. Crouse. In review. Assessment of burn severity using Landsat 7 ETM+ imagery and ground data. International Journal of Wildland Fire.

Chapter 2: Forest Change on the San Francisco Peaks, Arizona

By: Allison E. Cocke and Peter Z. Fulé

Introduction

Consequences of fire exclusion vary by forest type (Bekker and Taylor 2001, Whitlock et al. 2003). In the Southwest, the effects of fire exclusion associated with Euro-American settlement have been well studied in low elevation forests, mostly ponderosa pine, adapted to frequent fire regimes. In these areas, exclusion has resulted in high tree density, fuel accumulations, and increased risk of crown fire (Cooper 1960, Covington et al. 1994, Swetnam et al. 1999, Fulé et al. 2003). High elevation forests comprise only about 3% of Arizona forests (O'Brien 2002) but are ecologically critical sites for landscape diversity (Dahms and Geils 1997). The role of fire and the effects of fire exclusion have not been well studied in these rare forests, although fire is a key process of the landscape which affects species age, composition, and shifts in elevational ranges (Beaty and Taylor 2001).

Pre-exclusion fire regimes have been determined using fire scars and age data for other Southwestern ponderosa pine and mixed conifer stands. Estimated intervals include 2-12 years for ponderosa pine and 4-14 years for mixed conifer (summarized in Swetnam and Baisan 2003). In contrast, studies of spruce-fir forests described infrequent, high intensity fires, with intervals ranging from 70-400 years (Aplet et al. 1988, White and Vankat 1993, Grissino-Mayer et al. 1995, Fulé et al. 2003). Several hundred years may pass before large fires are possible in spruce-fir forests due to slow fuel accumulation and the requirements for extremely low moisture, in addition to an ignition source (Romme 1982, Habeck 1985, Bessie and Johnson 1995, Grissino-Mayer et al. 1995). Similarly, fuel accumulation is slow in bristlecone stands due to the short growing season and needle retention up to 45 years (Ewers and Schmidt 1981) which probably results in long fire intervals.

The type and extent of forest changes due to fire exclusion vary widely between forest types. Because ponderosa and mixed-conifer stands had frequent fire regimes, structure and composition have been dramatically altered as a result of fire exclusion (Covington and Moore 1994, Fulé et al. 2002). Species adapted to a frequent fire regime have high regeneration allowing at least some survival; without fire, an overabundance of trees are able to survive causing exceptionally high densities (Savage et al. 1996). Furthermore, mesic trees that would be most readily killed by fire are able to survive. Mesic species are also much more shade tolerant than ponderosa pine and can successfully establish beneath the existing canopy. Shade-tolerant conifers also successfully establish within aspen stands (Jones and DeByle 1985, Hessl 2002). Aspen vegetatively sprout with most regeneration occurring following large disturbances including fire. Without fire, less opportunity for abundant regeneration exists and aspen cover overall may be declining (Loope and Gruel 1973, Johnson 1994, Dahms & Geils 1997). Conversely, because spruce-fir and bristlecone forests experience naturally long fire intervals, it is possible that a century of fire exclusion has not had as large an impact as in lower elevation forest (Romme 1982). Throughout the Rocky Mountains and the Southwest, spruce-fir densities range from 980-1394 trees/ha (Veblen et al. 1991, White and Vankat 1993, Fulé et al. 2003) with high fuel accumulations (Aplet et al. 1988, Fulé et al. 2003). Very little is known about bristlecone forests. Baker (1992)

found that most forests in Colorado were greater than 500 years old and some greater than 750 years old with low fuel accumulations.

Ponderosa pine and mixed conifer may be more directly susceptible to changes caused by fire exclusion including potentially larger and more severe fires (Covington and Moore 1994, Sampson et al. 2000). Fire exclusion may also include decreased regeneration of aspen stands. Decline in aspen has been reported for decades and is well-studied (Johnson 1994, Renkin and Despain 1996, Kay 1997, Ripple and Larsen 2000). Less well studied are high elevation forests, although changes in these areas may also threaten their sustainability. While fire exclusion may have direct effects on these high elevations forests, climate change poses an even greater threat. Predictions for increased global temperatures have great implications for high elevation forests (Malcolm et al. 2002). Because of changes in fire regimes, the forests may not be prepared for increased temperatures which may lead to drought and therefore greater chance of fire (Flannigan et al. 2000). Rapid changes in climate may result in certain species being incapable of surviving (Shafer et al. 2001, Loehle 2000).

The San Francisco Peaks (hereafter "Peaks") in northern Arizona comprise a unique environment of great significance in ecological terms, as a "sky island" of habitat that represents all of the important high-elevation forest types of the Southwest, in scientific history as the site of Merriam's (1890) studies on elevational gradients, and in cultural terms as an area of great significance to several Native American tribes. The Peaks reach 3854 meters in elevation, the highest point in Arizona, with forest types including ponderosa pine, mixed conifers (including Douglas-fir and limber pine), aspen, Engelmann spruce-subalpine fir (an endemic variety called corkbark fir), and bristlecone pine. Scientific names of all species are given in Table 1. The Peaks support rare species including *Senecio franciscanus*, endemic to the San Francisco Peaks, and habitat for rare species such as the Mexican spotted owl, northern goshawk, and black bear. Fire was nearly completely excluded after 1876 or 1879 due to livestock grazing and fire suppression practices introduced by European settlers (Dieterich 1980, Heinlein 1996) with minimal areas burning since then (unpublished data).

The objectives of this study were to compare current and reconstructed forest structural patterns over the Peaks elevational gradient to address the following questions. 1) How has forest structure changed within each vegetation type after approximately 130 years of fire exclusion? We hypothesized that forests adapted to frequent surface fire would be the most severely altered, while high-elevation forests would show minimal change. 2) Has forest composition shifted over the landscape? We expected to find encroachment of fire-susceptible mesic species downward in the elevational gradient in the absence of fire. 3) Finally, since we applied nearly identical research methods on a steep elevational gradient on the Peaks as in previous studies on a gentle elevational gradient at Grand Canyon (Fulé et al. 2003), we hypothesized that steep topography of the Peaks would lead to more pronounced differentiation (reduced variability) within vegetation types and greater variability between types, compared to the Grand Canyon.

Methods

Study Area

We sampled an area of roughly 3500 hectares on the south side of the San Francisco Peaks within the Coconino National Forest, north of Flagstaff, Arizona (Figure 2.1). Study plots were within or adjacent to the Kachina Peaks Wilderness Area. Elevations ranged from 2442 meters to 3559 meters. Plots were measured from the year 2000 until 2003. Sampling took four years because plots all had to be reached on foot, forests were closed to research in 2000 and 2002 due to

extreme drought, and the Leroux Fire of 2001 also closed the forest for several weeks. Weather from the Fort Valley weather station (www.wrcc.dri.edu), located approximately five km southwest of the study site, was summarized using data from 1909-2001. Mean January temperatures were 5.2° C maximum and -12.3° C minimum. Mean July temperatures are 26.7° C maximum and 7.1° C minimum. Mean annual precipitation was 56.9 cm.

In this study, we stratified forest vegetation types into five categories: Ponderosa, Mixed conifer, Aspen, Spruce-fir and Bristlecone. Henceforth, these terms will be used to indicate the vegetation type. Individual tree species will be referred to by codes based on the genus and species, as shown in Table 2.1.

Because the Peaks form a steep elevational gradient, we were able to contrast forest structure and change since fire exclusion for different forest vegetation types in a relatively small area. Plots highest in elevation were generally 3 km away from lowest plots within the same transect and a distance of less than 7 km separated the two farthest plots in the study site. Therefore, while temperature and moisture varied naturally due to elevational differences, other factors affecting forest development were relatively consistent. The Wilderness Area was set aside in 1984, so recent impacts were mostly recreational. Past grazing occurred at all elevations but timber harvesting only occurred up to roughly 2700 m in elevation.

Forest Structure Sampling and Analysis

Field Method

Sampling was done on a systematic grid, measuring forest age structure and species composition proportional to occurrence over the landscape. One hundred thirty-five plots were located on a grid 300 m N-S and 300 m or 600 m E-W, in order to measure with greater sampling density along the prevailing elevation gradient, N-S (Figure 2.1). Non-forested grid points were discarded if points 50 m to the N, E, S, and W were also unsuitable. The grid spacing was designed to measure fire and forest structure at a large scale, consistent with the expectation of relatively large fire-initiated stands at higher elevations.

Sampling plots, based on the National Park Service's Fire Monitoring protocol (Reeberg 1995, NPS 2003), were 0.1 ha (20 x 50 m) in size, and were used to measure vegetation, fuels, and dendroecological data for reconstruction of past forest structure. Plots were oriented with the 50 m sides uphill-downhill to maximize sampling of variability along the elevation gradient and to permit correction of the plot area for slope. Plots were marked with iron stakes in centers and corners, and a tagged reference tree marking distance and bearing to plot center. Photographs were taken at corners and quarter-corners.

All trees were tagged and tree measurements included species, diameter at breast height (dbh), height, crown base height, and tree condition. Trees larger than 15 cm dbh were measured on the entire plot; trees between 2.5 and 15 cm dbh were measured on a 0.025 ha subplot. Trees smaller than 2.5 cm dbh were considered regeneration (seedlings and sprouts) and were tallied by species, condition, and height class on a 50m² subplot.

Tree cores were taken at 40 cm above ground level for all trees that were considered to have established before the time of fire exclusion and for 10% of trees that established after this period. Conifers with dbh = 37 cm, aspens with dbh = 20 cm, and PIPO trees of any size with yellowed

bark were likely to pre-date fire exclusion (White 1985, Mast et al. 1999, Fulé et al. 2002). Origin date was later corrected in the laboratory using age data.

Canopy cover measured by vertical projection (Ganey and Block 1994) was recorded along the 50-m sidelines; in 2000 this was done every 30 cm and in 2001-2003, it was done every 3 m. Forest floor and woody debris were measured along four 15.24 m planar intersect transects (Brown 1974), located every 10 m along the plot centerline. Transect directions were randomly chosen. Litter and duff depths were measured every 1.52 m along each transect, and wood debris was measured by time-lag classes (equivalent to diameter categories; Anderson 1982) of 1 hr, 10 hr, 100 hr, and 1000 hr along each transect.

Laboratory Methods

Plot areas were corrected for slope. Tree increment cores were surfaced and visually crossdated (Stokes and Smiley 1968) with tree-ring chronologies we developed (Graybill 1987). Rings were counted on cores that could not be crossdated, especially younger trees. Additional years to the center were estimated with a pith locator (concentric circles matched to the curvature and density of the inner rings) for cores that missed the pith (Applequist 1958). Past forest structure was reconstructed at the time of disruption of the frequent fire regime, 1876 (Dieterich 1980, Heinlein 1996), following dendroecological methods described in detail by Fulé et al. (1997, 2002). Tree diameter at the time of fire exclusion was reconstructed for all living trees by subtracting the radial growth measured on increment cores since fire exclusion. For dead trees, the date of death was estimated based on tree condition class using diameter-dependent snag decomposition rates (Thomas et al. 1979, Rogers et al. 1984) or historical harvesting records for stumps. Decomposition rates were calculated for average conditions (the "50th percentile" tree) as well as for fast decomposition (25th percentile) and slow decomposition (75th percentile) in order to assess the sensitivity of reconstruction results to decomposition rate. To estimate growth between the fire exclusion date and death date, we developed local species-specific relationships between tree diameter and basal area increment ($r^2 = 0.38$ to 0.92). Fuel loadings were calculated from the planar transect data (Brown 1974, Sackett 1980).

Vegetation was classified using a Landsat 7 Enhanced Thematic Mapper (ETM+) image from June 6, 2000. All image classification and analysis were done using ERDAS Imagine (Atlanta, GA). Sampling plot data were used as training sites for the classification process and were digitized directly on the ETM imagery. Each training site polygon included at least ten pixels including those that corresponded with each sampling plot center. A supervised classification using a minimum distance algorithm was used. The species label for each training site was based on 'importance value' (Taylor 2000) calculated as the sum of the relative frequency (density) and relative abundance (basal area). The imagery was classified into seven cover types including ponderosa pine, mixed-conifer, aspen, spruce-fir, bristlecone pine, meadow, and rock. In our study site, mixed-conifer stands were composed primarily of PIFL and PSME.

Statistics included descriptive statistics and correlation/regression to explore relationships between variables. Differences in structural characteristics on the same plots over time were compared with paired t tests after being logarithmically transformed using the equation $X' = \log(X+1)$ (Zar 1984) to meet assumptions of parametric tests. Data between forest types were compared with ANOVA. Fuels were transformed as above and Tukey was used to examine where differences between types existed. With logarithmic and square root transformations, seedlings distributions were still not normal, so the Kruskal Wallance test was applied. Alpha level for all analyses was 0.05.

Results

Ponderosa pine was the predominant vegetation type on the landscape with roughly 1043 ha, or 30.1% of the study area, according to the classified Landsat imagery. This was followed closely by aspen (29.5%), then mixed conifer (18.3%), bristlecone (12.5%) and spruce-fir (9.6%). The plot data distribution was a faithful representation of the landscape, as shown by comparison to the imagery data. Classified by importance value, 31.1% of the plots were dominated by aspen (Table 2.2). This was followed by ponderosa (22.2%), mixed conifer (22.2%), bristlecone (17.0%), and spruce-fir (7.4%).

Elevations ranged from ponderosa with an average of 2605 m, to bristlecone with an average of 3288 m. In between, average elevations increased from mixed conifer (2781 m), aspen (2837 m), and spruce-fir (3197 m). Slopes increased at higher elevations with ponderosa averaging 15.9% slope to bristlecone averaging 53.3%. Elevation and slope were highly positively correlated (Pearson, $r = 0.75$, $p = 0.00$). Most plots (45.9%) had a south aspect, with a few to the east (3.0%), west (9.6%), southeast (16.3%), and southwest (25.2%). All cover types had the greatest number of plots facing south with the exception of spruce-fir (Table 2.2).

Most tree species occurred within all forest types but ponderosa, bristlecone, and spruce-fir, did not include all seven tree species. No ABLA occurred in the ponderosa forest type, no PIPO and PSME were found in the bristlecone forest type, and no PIPO occurred in the spruce-fir forest type. One species clearly dominated in both density and basal area in most forest types. For example, in the ponderosa pine cover type, 87% of the density and 88% of the basal area were made up of PIPO with the remainder comprised by PIFL, PSME, and POTR. Compositional mixing was highest in the mixed conifer cover type where POTR was 22% of the density and 19% of the basal area. PIEN also comprised a large percentage of the density in the bristlecone forest type (31%) although PIEN trees were relatively small, making up only 14% of the basal area in this forest type.

Overall, density was greatest in spruce-fir (840.3 trees/ha) and least in bristlecone (546.0 trees/ha) (Table 2.3). Basal area was also highest in spruce-fir (57.8 m²/ha) but lowest in ponderosa pine (34.4m²/ha). The highest percent canopy cover was in mixed conifer (65.7%) followed by aspen (63.6%); lowest was bristlecone (39.3%) (Table 2.4). Litter depths ranged from an average of 0.73 cm in the bristlecone pine forest type to 1.62 cm in the ponderosa pine forest type. Duff depths were all greater than litter. Duff was lowest in bristlecone forests (1.79 cm), but was highest in spruce-fir forests (4.32 cm). Total woody debris was quite variable by forest type, ranging from 62.04-132.19 Mg/ha (Table 2.5). Tree density was highly correlated with fine fuels (r ranged from 0.189 to 0.425, p ranged from 0.00-0.028).

Greatest regeneration density occurred in the aspen forest type, with a total of 2580 stems/ha, mostly POTR (Table 2.6). The bristlecone forest type had the lowest regeneration density (301.5 stems/ha, mostly PIAR). These two species followed the same trend regardless of forest type, with POTR regenerating the most (775 stems/ha) and PIAR the least (25 stems/ha). Most stems were in small height classes. Total regeneration was highest for all species in the height class less than 30 cm, ranging from 127 stems/ha in bristlecone to 1766 stems/ha in aspen stands. For stems between 30 cm and 2 m, density was lower in all forest types except bristlecone. These ranged from 174 stems/ha in bristlecone and 739 stems/ha in aspen stands. Densities were lowest for all stems taller than 2 meters. No stems in this height class occurred in bristlecone or spruce fir stands, and other values were 72 stems/ha for mixed conifer, 35 stems/ha for ponderosa, and 44

stems/ha for aspen. All stems in the aspen type greater than 2 meters were all PIFL or PSME, meaning that there was a complete absence of POTR regeneration taller than 2 m. Therefore, although POTR sprouts made up the highest density of all species, all were smaller than 2 m. Seedlings of several species were positively correlated with canopy cover, including ABLA, PIFL, POTR, and PSME (r ranged from 0.183 to 0.250, p ranged from 0.004-0.036). Of seedlings, the only correlations to ground fuels were that PIAR was negatively correlated with litter ($r = -0.169$, $p = 0.05$), and that PSME was affected by most ground fuels including duff ($r = 0.311$, $p = 0.00$), 1 HR ($r = 0.197$, $p = 0.022$), and 10 HR fuels ($r = 0.220$, $p = 0.01$).

Age distributions were calculated in 20 year intervals by species (Figure 2.2). PIAR have been steadily establishing for the last 400 years. The spruce-fir species (PIEN and ABLA), as well as the mixed conifer species (PSME and PIFL), also experienced continuous establishment. POTR and PIPO had more variable establishments. POTR experienced a large increase around 1880 following by a decline; few POTR have established since the 1940s. PIPO had a large increase in establishment around the 1920s and 1940s.

All forest types had significantly lower densities and basal areas in 1876 than in 2000 (paired t test, $p=0.000$) (Table 2.8). Overall tree densities in 1876 ranged from 61.7 trees/ha in ponderosa pine to 283.9 trees/ha in bristlecone pine. Basal areas ranged from 7.3 m²/ha in aspen to 27.3 m²/ha in bristlecone pine. Density increases were largest in ponderosa pine (1073%) and lowest in bristlecone pine (92%). However, changes in basal area were greatest in aspen stands (456%) and lowest in bristlecone pine stands (69%) (Table 2.8). Greatest density increases were the conifers PIEN, ABLA, and PSME in aspen forests, PSME in ponderosa forests, and PIFL in bristlecone stands. The only decrease that occurred anywhere in the study site was a decline in PIPO density and basal area in the aspen cover type. Several species now occur in forest types in which they previously did not occur. In the 1876 forest, ABLA, PIAR, PIEN, and PIFL were missing from the ponderosa forest type and PIPO was missing from bristlecone and spruce-fir forest types. By 2000, PIPO was still missing from bristlecone and spruce-fir forests, but ABLA was the only species missing from ponderosa forest types. By matching 1876 distributions with plot elevations, we found that ranges of POTR remained the same elevationally. However, PIAR has descended by 150 meters, PIEN by 400 meters, PIFL by 25 meters, and PSME by 55 meters. In 1876, PIPO's upper limit was 3029 meters, but currently the upper limit for this species is 2860 meters. However, some ascents have also occurred; ABLA and PIFL are currently found 200 and 156 meters higher, respectively, than in 1876.

Discussion

Accuracy of Data and Reconstruction

Several potential sources of error exist in the 1876 stand reconstruction, including loss of evidence and the use of generalized decomposition equations for dead trees. Loss of evidence would be largest if a fire had occurred in the study site after the reconstruction date. Fire scars and age data collected in a companion study show that almost no fires occurred on the study site after 1876 or 1879 (P.Z. Fulé unpublished data). Loss of evidence could also occur if small trees or clumps of small trees decayed completely. Small trees are most likely to be missing from the reconstruction as they could have decayed within a 125 year period. However, as in Fulé et al. (2003), if we assume that all of the trees in the present forest less than 15 cm in diameter were present in the 1880 forest, the density would increase by 300 trees/ha and the basal area would increase by 1.8 m²/ha. This increase is relatively low and likely represents the maximum possible error. The methods we applied on the Peaks have been tested in other northern Arizona forests.

Mast et al. (1999) showed that old tree material could be reliably dated to pre/post-1876 status in the field. Moore et al. (in press) compared historical tree records (1909) to reconstructed ponderosa density, finding that roughly 3 trees/ha were lost in the reconstruction, likely due to decay. Fulé et al. (2003) compared reconstructed forest structure, including PIPO, PSME, ABLA, and PIEN, to data from a detailed survey done by Lang and Stewart in 1910 on the North Rim of Grand Canyon. Tree density in the 1910 survey data averaged 5-9% of the reconstructed data, and no species exceeded 25% difference. Donnegan and Rebertus (1999) reconstructed forests in upper subalpine xeric stands in Colorado. By aging live and dead trees, they determined that decay was slow enough to effectively reconstruct these stands for longer periods than those determined for mesic areas.

Generalized decomposition equations also add uncertainty to the reconstruction model, leading us to carry out a sensitivity analysis using three different decomposition rate percentiles, 25, 50, and 75%. Changes in stand densities in the five forest types ranged from 1.3%-16.6% between the 25th and 50th percentiles. Differences were between 7.0% and 14% between the 50th and 75th percentile. Changes in basal area ranged from 0.1% -21.2% between 25th and 50th percentiles. Differences were between 10.8% and 22.6% between the 50th and 75th percentiles. Reconstruction is more sensitive in certain forest types than others. Density differences between the 25th and 50th percentile were small for all forest types (less than 5%) except aspen (17%), whereas basal area differences were 21% for spruce-fir, 13% for ponderosa, 6% for bristlecone, and there was no change in mixed conifer. Density differences between the 50th and 75th percentile were lowest in bristlecone (7%) while mixed conifer was highest (14%). Basal area differences were high ranging from bristlecone (11%) to spruce-fir (22%).

The most effective assessment would be to compare our data with any historical data; unfortunately, little historical data exist on the San Francisco Peaks except for the ponderosa pine forest (Avery et al. 1976). Past surveys were descriptive with little quantitative data (Merriam 1890, Little 1941, Moore 1965). Timber surveys (Leiberg et al. 1904, USFS Timber Atlases on file at Supervisor's Office, Coconino National Forest) were carried out in lower elevations, as high elevation forests had little timber value and slopes were too steep to harvest. Nonetheless, Leiberg's 1904 survey, done 20 years after our reconstruction date, offers some quantitative data in the form of average tree diameters and elevational distributions. Leiberg et al. (1904) used the Michigan practice of estimating timber, so they only included trees with diameters greater than 8 inches at a height of 2 feet from the ground. Direct comparison is difficult due to missing data and different methods of measurement (Table 2.9).

Quantitative measurements of density were not included in Leiberg et al.'s (1904) study, but they described many "parks" where no trees grew: "a yellow-pine forest, as nearly pure as one in this region, always has an open growth, but not necessarily as lightly and insufficiently stocked as is the case in this forest reserve" (Leiberg et al. 1904:23). This was an observation regarding the whole reserve and not just the part encompassed by our study. In contrast, at higher elevations "the forest which forms the transition type consists of closely stocked stands, whose density is due to great quantities of aspen of all ages, in which the coniferous species are set in small groups...the subalpine type of forest at its lower elevations is formed of closely stocked stands..." (Leiberg et al. 1904:19-20). These observations are consistent with our reconstruction of ponderosa dominated stands as extremely open, and other forest types as already quite dense, in 1876.

Forest structural changes

Changes in tree density and basal area were smallest in higher elevation forests between 1876 and today, supporting our first hypothesis about forest change. Changes in bristlecone forests were lower than all other forest types on the Peaks. These forests have discontinuous and minimal fuel loadings (Ewers and Schmidt, 1980). PIAR has a high fire tolerance rating (USDA 2004) but was classified in the “no predictable fires” group by Keeley and Zedler (1998). Mature PIAR on the Peaks may have survived fires over the last several centuries as current forests are characterized by large and old trees, several with multiple fire scars (unpublished data). While Baker (1992) determined that bristlecone in Colorado established primarily following fire, we found continuous establishment of PIAR for over 400 years. At the plot level, there were generally several hundred years separating the oldest trees from the most recently established, with continuous establishment in between. Preliminary fire regime data from PIAR on the study area indicated evidence of both surface and small patches of stand-replacing fire (P.Z. Fulé and others, unpublished data).

Density changes in the spruce-fir forest type were low compared to lower elevation forests despite lack of fire. Because ABLA and PIEN are relatively fire-susceptible, ages of old trees are often considered to indicate fire-free intervals, although varying patterns of establishment (Merkle 1954, Aplet et al. 1988) make it difficult to determine when the last fire occurred. From ages of oldest trees, we can estimate that a stand-replacing fire has not occurred for at least 200 years in most of the Peak's spruce-fir forest. Stromberg and Patten (1991) considered the 100-200 year period as shifting from “closed-pole stage” to “mature”. Because it has likely been several centuries since a large portion of the spruce-fir areas have burned, it follows that these forests have great duff and coarse woody debris accumulation. Litter depths and fine fuel loadings were low which could be due to a compact litter layer (Silvics 1990) and retention of dead branches (Brown and Bevins 1986).

Mixed conifer stands had moderate density increase and relatively low increase in basal area. Peaks age data shows establishment of PSME (ca. 1600) a century before PIFL (ca. 1700). However, plot data show no order of establishment; in some cases PSME established first and in other cases PIFL was first. Both have had continuous establishment through the present. For mixed conifer stands, past quadratic mean diameter (QMD) was 27.7 cm for POTR, 40.7 cm for PIFL, and 38.4 cm for PSME. Current QMD was 26.9 cm for POTR, 35.4 cm for PIFL, and 33.5 cm for PSME. QMD of all species were generally smaller in the current forest.

Aspen stands showed large density increases, only second to ponderosa stands. 1876 densities of other species were much lower than POTR density and remain low in 2000, except for PSME which is somewhat dominant in the aspen cover type. This relates to compositional changes as discussed below. QMD for the past aspen forests were 31.2 cm for POTR, 36.5 cm for PIFL, and 38.5 cm for PSME. For the current aspen forest, QMD was 30.9 cm for POTR, 31.9 cm for PIFL, and 30.6 cm for PSME. Again, POTR values are similar between 1876 and the current forest while decreases were larger in PSME and PIFL. Oldest POTR center dates ranged from 1779-1919 with most center dates from the mid 1800s. Over 84% of dead trees within aspen forest types were actually POTR, demonstrating the decadence of aspen stands.

Ponderosa pine forests have changed the most in density and also have high changes in basal area, although not as high as increases in aspen stands. The percent density increase between 1876 and the current forest is more than twice as much as any other cover type. Current ponderosa stands on the Peaks have moderate densities compared to other forest types, but have low basal areas, indicating establishment of many small trees. PIPO establishment was low but continuous until around 1880, when establishment escalated. Establishment was even greater in the mid 1900s. Successful regeneration for the past 120 years is consistent with fire scar

information for this forest type (Dieterich 1980, Heinlein 1996) as well as studies from nearby stands (White 1985, Mast et al. 1999). Current regeneration on the Peaks is highly PIPO and POTR, with little PSME and PIFL. Meadow invasion has occurred in many lower elevation parks (Dyer and Moffett 1999). On the Peaks, plots where oldest trees established after 1920 were along meadows.

Although change has clearly been greater in certain forest types, the whole landscape is affected by forest change. Because changes were lowest in high elevation forests, fire exclusion has probably had less impact on these areas (Romme 1982) although even limited effects might be ecologically meaningful (Taylor 2000). Fire exclusion could affect high elevation fire regimes simply due to changes in low elevation regimes. Fulé et al. (2003) found that fire years in higher elevations were also fire years in lower elevations, as many ignitions in lower forests were carried upslope. In cedar groves, Habeck (1985) found that although stands that experience fire infrequently may have had few direct effects of fire exclusion, these forests are often adjacent to forest types that have been highly affected by exclusion, creating more continuity. White and Vankat (1993) noted that the continuity of dense stands in a high-elevation forest could lead to larger fires, perhaps creating landscapes with less patch diversity. Grissino-Mayer et al. (1995) suggested that the mixed conifer forests acted as a buffer around spruce-fir forests.

Climate change also causes forest change (e.g., Shafer et al. 2001) and can interact with those changes caused by fire exclusion. Dyer and Moffet (1999) suggest that climatological change, rather than changes in fire regime, caused meadow invasion by spruce and fir. This was evidenced by invasion only on southern aspects with northern aspects maintaining stable boundaries. Likewise, Little (1941) found that the treeline was much higher on the southern side of the San Francisco Peaks than on the northern side. The role of climate change in the twentieth century on the Peaks is not entirely clear. Salzer's (2000) dendroclimatological reconstruction from the Peaks found that periods in the early and late twentieth century were relatively wet, but Biondi (1999) observed no trend in twentieth century weather records from Fort Valley, at the base of the Peaks. While it may not be possible to disentangle the past influences of climate from those of fire exclusion, however, the predicted future climate is likely to pose a sharply different environment with negative effects on current forest conditions, as described below.

Composition Shifts

As we hypothesized, the lack of fire was associated with a shift in species composition, resulting in greater dominance by mesic species at lower elevations compared to 1876. Regeneration of ponderosa pine is low in heavily forested areas (Arno et al. 1995) whereas shade-tolerant species are more successful (Camp 1999, Fulé et al. 2003). Without fire, trees of these species were able to survive where establishment was previously prevented. In 1876 ABLA, PIAR, PIEN, and PIFL did not exist within the ponderosa forest type. However, in 2000, all of these species except ABLA occurred in the ponderosa type. This trend did not occur in the opposite direction; no lower elevation species were found in sites where they were nonexistent in 1876.

Shade-tolerant conifers increased in mid elevation forests; not only have PIFL and PSME become more dominant in mixed conifer forests, but aspen stands are also being invaded by conifers. Numerous studies have suggested that aspen cover is declining in the West. Johnson (1994) estimated that aspen stands declined by 46% in a 24 year period in New Mexico and Arizona. Because aspen regenerate best following disturbances (Dahms and Geils 1997) and poorly without disturbances (Andrejak and Barnes 1969), fire exclusion has likely had a negative impact on these stands. Recent studies in Yellowstone showed a rare occurrence of aspen seed sprouts

following the fires of 1988. In this case, aspen were found in burned sites almost 15 km away from adult aspen, leading to range expansion (Romme et al. 1997, Turner et al. 2003). However, warm temperatures will reduce moisture conditions preventing seeds from establishing. Moisture conditions are rarely met as occurrence of seed sprouts did not follow other major Yellowstone fires within the same century. Furthermore, high numbers of elk decimate any regeneration (Bartos et al. 1994, Kay 1997, Ripple and Larsen 2000, Hessler and Graumlich 2002). However, the Peaks sample plots and satellite imagery show that aspen is still a dominant cover type and aspen stands include higher densities and regeneration. Despite its current dominance, POTR age data showed that within 50 years of fire exclusion, POTR establishment severely decreased and invasion of conifers occurred so that a much higher percent of the trees are now conifers than in 1876. Similar to numerous studies (e.g. Ripple and Larsen 2000), most (93%) successful establishment of aspen on the Peaks occurred before 1920 showing the decadence of current stands. As these stands start to break up, root densities decrease leading to decreased possibility of vegetative sprouting (Schier 1975, Shepperd et al. 2001). Several studies have found that higher aspen mortality also relates to higher aspen regeneration. Removal of all stems may result in the more sprouting (Bartos et al. 1994, Bailey and Whitham 2002). However, these studies also found that areas of most re-growth were consistently the ones most browsed upon by elk, thereby greatly reducing the numbers.

Other compositional shifts have occurred in other areas of the West. Because PSME does not establish readily under high amounts of shade (Merkle 1954), lack of disturbance has been known to shift forest composition to spruce-fir (Stromberg and Patten 1991). This does not appear to be happening on the Peaks. There has been a very slight decrease in spruce-fir species (2% to 1.4%) and ABLA and PIEN sprouts are nonexistent in the mixed conifer cover type. Some studies show that PIFL is usually overtaken or co-dominates with other species, such as Douglas-fir (Layser and Schubert 1979). The ratio of PIFL density to PSME density is similar in 1876 to the present forest; therefore, there is no evidence that one is overtopping the other. High numbers of aspen within mixed conifer plots support Kay's (2003) study suggesting that small patches of aspen exist with other species. While encroachment of fire-susceptible species is usually into lower elevations, PIEN appears to be encroaching in bristlecone forests. While the PIAR and PIEN often co-dominate (Baker 1992), regeneration data shows that there are more PIEN sprouts than PIAR. With time, bristlecone stands may shift to different forest types, especially spruce-fir (Schubert and Rietveld 1970), although this process can take over 1000 years (Baker 1992).

Fire and Climate Interactions

Climate interacts with disturbance, influencing how and when forests burn (Turner et al. 1994, Swetnam and Baisan 2003). Past warm periods created severe drought conditions leading to high fire activity (Whitlock et al. 2003). Many studies suggest that global temperatures will continue to increase (Hansen and Weltzin 2000, Flannigan et al. 2001), leading to increases in fire frequency and severity (Whitlock et al. 2003) due to more "extreme temperature days", increased drought (Hansen and Weltzin 2000), and longer fire seasons (Flannigan et al. 2001).

Climate changes combined with fire exclusion have major implications for Southwestern forests. Increased temperatures cause lower elevations to become too dry to support some species (Shafer et al. 2001), which may migrate to higher elevations if natural and/or human-aided migration rates are fast enough (Malcolm et al. 2002). High elevation forests, which usually retain higher moisture content, will become drier and more likely to burn. However, fire exclusion has caused a downward movement of species, the exact opposite of what would occur over a long period of warming. Therefore, fire exclusion has altered the forests in exactly the wrong direction for being

resilient to climate change. Without fire exclusion, mesic species would probably not have migrated down in elevation and would not be as susceptible to increased fire. However, because species have moved down in elevation, fire threatens more forest types and their dependent species. Rapid climate change may already be difficult for plant communities to cope with (Shafer et al. 2001, Malcolm et al. 2002), but results of fire exclusion have made difficulties greater, potentially leading to massive shifts in biodiversity.

Comparison between Peaks and Grand Canyon

The steep elevational gradient of the Peaks was associated with less variability within forest types and more between forest types than the gentle gradient at Grand Canyon (Fulé et al. 2003). Average slope by vegetation type at Grand Canyon ranged from 14-19%, while on the Peaks, slopes ranged from 16-43%. The Grand Canyon site also had a more narrow range of elevation, with all plots falling between 2600-2700 m. Each vegetation type at the Peaks study area was predominantly comprised of only one or two species. For example, the ponderosa forest type was mostly composed of PIPO, and the spruce-fir forest type was mostly composed of PIEN and ABLA. In contrast, much greater mixing of species occurred within forest types at Grand Canyon. For example, PIPO density was only 29% of the ponderosa cover type, compared to the Peaks where this value is 87%. Furthermore, POTR and all the conifer species occurred in every single forest type at Grand Canyon, while on the Peaks species on one end of the elevational gradient did not appear in forest types on the other end of the gradient (e.g. no ponderosa pine in bristlecone and spruce-fir cover types). Reconstructed forest densities in 1876 or 1880 at Grand Canyon were all higher than the Peaks, except for spruce-fir which was considerably higher on the Peaks (266 vs. 150 trees/ha). The largest difference was in ponderosa pine, with only 62 trees/ha on the Peaks compared to 337 trees/ha at Grand Canyon. Current densities for all forest types were lower on the Peaks than at Grand Canyon, where values were 1382 trees/ha for aspen, 873.4 trees/ha for mixed conifer, 782.3 trees/ha for ponderosa pine, and 946.0 trees/ha for spruce-fir. However, basal areas were lower for all forest types at the Grand Canyon, where values ranged from 27.8 m²/ha to 38.8 m²/ha. Thus trees tended to grow more densely but have smaller average diameters at Grand Canyon.

Regeneration was much greater at the Grand Canyon, ranging from 5128-12,271 stems/ha, whereas on the Peaks these values were much lower (approximately 300-2,600 stems/ha). Regeneration was also grouped more tightly within distinct forest types at the Peaks. As an example, on the Peaks, ABLA seedlings did not occur in bristlecone, mixed conifer, or ponderosa cover types, while at Grand Canyon ABLA seedlings existed in all forest types. Herbivory may be a factor in constraining regeneration at the Peaks, because there are very few elk on the North Rim. This is especially probable in the case on aspen, where values on the Peaks were 2580 stems/ha compared to over 12,000 stems/ha on the North Rim.

Total woody debris was slightly lower on the Peaks than Grand Canyon but forest types followed similar patterns at both sites, with ponderosa having the lowest woody biomass (note that the bristlecone type did not exist at Grand Canyon) and spruce-fir the highest. Litter depths were nearly identical between the two sites but duff was generally deeper on the Peaks and much more distinct between forest types.

Management implications

Fire exclusion has resulted in large changes in certain forest types. The impact is probably most pronounced on organisms that depend on particular structure and composition (Romme 1982, Dahms and Geils 1997). For instance, Hutto (1995) showed that the effects of fire exclusion in the northern Rockies were disproportionately severe on certain bird species that relied on large snags. The negative consequences of forest change in ponderosa pine forests, such as increasingly large and severe wildfires (Swetnam et al. 1999), have led to calls for restoring more nearly natural conditions through thinning and burning (e.g., Covington 2000, Allen et al. 2002). Across the entire elevational gradient of a mountain range such as the Peaks, however, the management situation is more complex. Fire exclusion on the Peaks has resulted in increases in density and basal area to differing degrees depending on the forest type and compositional shifts include invasions of conifers in aspen and ponderosa stands, and movements of species into lower elevations. Compositional shifts may increase stand homogeneity which in turn can increase susceptibility not only to fire, but also to other disturbances such as pathogens.

Especially in ponderosa pine forests, structure and composition could be restored to conditions more similar to historical conditions through forest thinning and re-introduction of a surface fire regime. Combinations of thinning and burning have occurred in the Fort Valley area at the base of the Peaks, immediately adjacent to the southern border of our study area. The Fort Valley area was chosen for these treatments because it included dense forests and a high incidence of human-caused fire ignitions due to heavy recreational use and proximity to human communities. This area was also chosen specifically to reduce the threat of stand-replacing fires on the San Francisco Peaks (USDA Forest Service 1998). There is concern that a fire on the San Francisco Peaks will have similar results to the Pumpkin Fire of 2000 which burned on nearby Kendrick Mountain. This fire started in ponderosa pine forest and spread into higher elevations, eventually burning over 6000 hectares and destroying Mexican spotted owl protected areas and northern goshawk post-fledgling areas (Farnsworth 2002).

Fire on the Peaks is inevitable. Because it has been one to several centuries since higher elevation forests have burned, they have fuel loads conducive to burning during drought years. The Leroux fire of 2001 remained small with limited areas of crowning, but moisture levels were near average so the fire was unable to carry through aspen and into spruce-fir stands. In drought years, these forest types are unlikely to stop the fire. Even if treated areas at the base of the mountain do prevent fire from reaching higher elevation forests, fires will start eventually, whether lightning- or human-caused. Few fuels breaks exist: few roads, no rivers, minimal rocky areas until very high elevations. Slopes are extremely steep with several deep ravines which would make suppression efforts costly and extremely dangerous. Moreover, the premise of "restoring" natural conditions takes on a different context when the natural fire regime was one of infrequent, high-severity fires. Since several hundred years may pass between large fires in aspen and spruce-fir forests, they may still be within their range of natural variability (Romme 1982, White and Vankat 1993).

Aspen management needs to be considered in light of the high degree of elk herbivory (Bailey and Whitham 2003), resulting in a complete failure of aspen to reach sapling size in our study area. Severe fire can lead to aspen regeneration, but experience in the nearby Hochderffer Fire of 1996 showed that all aspen were killed except for those protected by high fences. Fencing is expensive, time consuming, and can only protect small areas. In contrast, aspen response has been vigorous following fire on the Kaibab Plateau at Grand Canyon, where only a small elk herd exists (Fulé et al. in press). Currently, most aspen on the Peaks are over a century old and regeneration has been unsuccessful. High amounts of coarse woody debris may enable some

aspen to survive out of reach of elk. Burning within the next few decades may give aspen a chance to regenerate vegetatively although this will entail extremely careful wildlife management, or else more harm can be done by burning (Bartos et al. 1994).

Table 2.1 Tree species found on study plots. Species codes were created from the first two letters of the genus and species names. White fir and Gambel oak were found sparsely in the study area but were not encountered on sampling plots. We called the low-elevation white pine *Pinus flexilis*, following Mitton (2000), but there is uncertainty about the presence of *Pinus strobiformus* or a zone of hybridization between *flexilis* and *strobiformus* on the San Francisco Peaks.

	Common Name	Code
<i>Abies concolor</i> (Gordon & Glendinning) Hoopes.	White fir	ABCO
<i>Abies lasiocarpa</i> var <i>arizonica</i> (Hook.) Nutt	Corkbark fir	ABLA
<i>Pinus aristata</i> Engelm.	Bristlecone pine	PIAR
<i>Picea engelmanni</i> Parry ex Engelm.	Engelmann spruce	PIEN
<i>Pinus flexilis</i> James	Limber pine	PIFL
<i>Pinus ponderosa</i> var. <i>scopulorum</i> P. & C. Lawson	Ponderosa pine	PIPO
<i>Populus tremuloides</i> Michx.	Quaking aspen	POTR
<i>Pseudotsuga menziesii</i> (Mirb.) Franco var. <i>glauca</i>	Douglas-fir	PSME
<i>Quercus gambelii</i> Nutt.	Gambel oak	QUGA

Table 2.2. Characteristics of forest vegetation types and sample plots.

Forest Type	Area (ha)	Average Elevation (m)	Number of Sample Plots	Average Slope (%) on plots	E Aspect	SE Aspect	S Aspect	SW Aspect	W Aspect
Aspen	1020.2	2867	42	31	1	8	15	11	7
Bristlecone pine	432.5	3287	23	53	1	8	10	3	1
Mixed Conifer	633.2	2781	30	31	2	3	17	5	3
Ponderosa pine	1042.6	2604	30	16	0	2	20	8	0
Spruce-fir	330.5	3197	10	41	0	1	0	7	2
Subtotal	3459		135		4	22	62	34	13
Grass	152.6								
Rock	135.4								
Total	3747		135						

Table 2.3. Density and basal area divided by forest type for current forest structure.

Forest Type	ABLA	PIAR	PIEN	PIFL	PIPO	POTR	PSME	Total
<i>Tree Density (trees/hectare)</i>								
Aspen	52.15 (30.3)	35.07 (16.2)	46.29 (31.7)	83.71 (20.6)	8.51 (3.3)	432.9 (37.2)	110.04 (38.6)	768.67 (94.0)
Bristlecone pine	0.95 (0.7)	342.61 (34.6)	169.49 (43.4)	12.84 (4.1)	0	20.13 (17.3)	0	546.02 (69.8)
Mixed Conifer	9.08 (6.0)	9.64 (8.5)	2.18 (1.9)	272.45 (40.3)	28.24 (10.7)	176.57 (321)	322.78 (51.5)	820.94 (76.7)
Ponderosa pine	0	0.35 (0.35)	0.34 (0.3)	29.93 (6.4)	626.32 (96.5)	18.07 (14.3)	49.08 (23.8)	724.07 (116.5)
Spruce fir	297.92 (89.3)	95.56 (51.1)	368.44 (81.9)	6.47 (4.6)	0	66.28 (34.1)	5.59 (5.6)	840.26 (138.0)
<i>Basal Area (m2/hectare)</i>								
Aspen	1.969 (1.0)	1.705 (0.9)	1.25 (0.7)	4.019 (0.8)	0.856 (0.3)	30.221 (2.0)	4.031 (0.9)	44.055 (2.5)
Bristlecone pine	0.131 (0.1)	38.324 (4.1)	6.46 (1.4)	0.523 (0.3)	0	0.767 (0.7)	0	46.207 (4.8)
Mixed Conifer	1.094 (0.7)	0.407 (0.3)	0.151 (0.1)	15.675 (2.2)	1.877 (0.6)	8.69 (1.1)	17.36 (3.0)	45.254 (4.2)
Ponderosa pine	0	0.007 (0.007)	0.012 (0.012)	1.506 (0.4)	30.394 (2.9)	0.532 (0.3)	1.99 (0.8)	34.439 (3.0)
Spruce fir	20.963 (5.5)	7.173 (3.0)	24.965 (4.9)	0.119 (0.09)	0	2.891 (1.5)	1.667 (1.7)	57.776 (4.2)

Table 2.4. Canopy cover (%) by forest type.

Forest Type	Mean	Standard Error	Minimum	Maximum
Aspen	63.6	2.9	25	97.6
Bristlecone pine	39.3	4.2	0	75
Mixed Conifer	65.7	3.5	18.8	96.9
Ponderosa pine	50.9	3.3	18.8	86
Spruce-fir	58.2	4.6	28.1	80.1

Table 2.5. Forest floor (litter and duff) depth and woody debris. Woody materials are listed by timelag class (1H = 1 hour timelag), corresponding to diameter categories (Anderson 1982).

Forest Type	Litter Depth (cm)	Duff Depth (cm)	1H (Mg/h)	10H (Mg/h)	100H (Mg/h)	1000H Sound (Mg/h)	1000H Rotten (Mg/h)	Total Woody Debris (Mg/h)
Aspen	1.09 (0.1)	2.64 (0.2)	0.22 (0.03)	1.6 (0.2)	6.46 (0.6)	41.05 (6.2)	44.88 (13.0)	94.21 (16.6)
Bristlecone	0.73 (0.1)	1.79 (0.3)	0.38 (0.06)	1.03 (0.2)	2.99 (0.7)	26.87 (7.2)	30.78 (14.6)	62.04 (19.5)
Mixed	1.23 (0.1)	3.82 (0.3)	0.33 (0.04)	2.82 (0.5)	7.42 (1.1)	32.24 (9.3)	29.61 (6.4)	72.41 (13.2)
Conifer								
Ponderosa	1.62 (0.2)	2.46 (0.3)	0.23 (0.04)	1.46 (0.2)	3.03 (0.5)	28.01 (16.3)	36.84 (17.1)	69.57 (25.0)
Spruce Fir	1.05 (0.2)	4.32 (0.8)	0.69 (0.1)	2.29 (0.8)	5.07 (1.1)	55.49 (24.3)	68.66 (38.8)	132.19 (51.9)

Table 2.6. Tree regeneration (stems/ha) by forest type. All classes of regeneration from stems < 15 cm in height to saplings < 2.5 cm dbh are grouped together.

Forest Type	ABLA	PIAR	PIEN	PIFL	PIPO	POTR	PSME	Total
Aspen	390.4 (339.4)	0	0	92.6 (49.8)	4.8 (4.8)	1975.1	117.3 (57.1)	2580.24
Bristlecone	0	118.6	133.5	20.3 (14.0)	0	29.2 (29.2)	0	301.49 (93.8)
Mixed	0	7.4 (7.4)	0	217.6 (124.9)	27.6 (27.6)	1431 (510.0)	180.6 (57.6)	1864.14
Conifer								(499.5)
Ponderosa	0	0	0	33.7 (23.9)	533.7 (284.6)	221.6 (152.6)	40.7 (15.1)	829.61 (321.7)
Spruce-Fir	218.8 (98.0)	0	173.2	0	0	217.9 (148.7)	153.5 (153.5)	763.37 (294.5)

Table 2.7. Reconstructed forest structure in 1876, based on dendroecological sampling and decomposition modeling.

Forest Type	ABLA	PIAR	PIEN	PIFL	PIPO	POTR	PSME	Total
<i>Tree Density (trees/hectare)</i>								
Aspen	2.2 (1.25)	9.1 (4.74)	0.8 (0.44)	9.2 (2.82)	9.5 (4.00)	101.2 (12.70)	9.8 (2.76)	141.8 (12.03)
Bristlecone pine	0.5 (0.50)	259.2 (33.16)	19.8 (7.1)	0.5 (0.51)	0	3.9 (3.89)	0	283.9 (35.75)
Mixed Conifer	2.4 (1.64)	2.4 (1.44)	0.4 (0.4)	43.8 (8.18)	18.3 (5.20)	45.2 (7.44)	50.6 (10.03)	163.1 (16.78)
Ponderosa pine	0	0	0	0	57.9 (6.38)	2.7 (1.51)	1.1 (0.83)	61.7 (6.47)
Spruce fir	62.0 (21.64)	87.8 (39.62)	100 (27.04)	2.2 (2.24)	0	9.6 (3.65)	4.5 (4.47)	266.2 (40.91)
<i>Basal Area (m2/hectare)</i>								
Aspen	0.26 (0.15)	0.75 (0.39)	0.03 (0.02)	1.14 (0.58)	1.12 (0.50)	2.44 (0.59)	2.17 (0.68)	7.92 (1.15)
Bristlecone pine	0.01 (0.01)	26.53 (3.58)	0.71 (0.34)	0.003 (0.003)	0	0.03 (0.03)	0	27.30 (3.71)
Mixed Conifer	0.24 (0.24)	0.26 (0.17)	0.001 (0.001)	4.64 (0.85)	2.06 (0.60)	0.65 (0.13)	10.03 (2.71)	17.89 (2.94)
Ponderosa pine	0	0	0	0	7.20 (1.09)	0.06 (0.04)	0.31 (0.22)	7.57 (1.13)
Spruce fir	2.63 (0.97)	8.05 (3.62)	3.67 (1.04)	0.05 (0.05)	0	0.11 (0.06)	0.97 (0.97)	15.47 (3.28)

Table 2.8. Matrix of percent change in tree density and basal area by forest types between 1876 and 2000.

Forest Type	ABLA	PIAR	PIEN	PIFL	PIPO	POTR	PSME	Total
			<i>Density Change (%)</i>					
Aspen	2241	285.4385	5887	807	10	327	1024	442
Bristlecone pine	93	32	753	2425	0	417	0	92
Mixed Conifer	284	301	452	522	53	290	537	403
Ponderosa pine	0	0	0	0	980	581	4233	1072
Spruce-fir	380	8	268	189	0	588	25	215
			<i>Basal Area Change (%)</i>					
Aspen	648	126	4494	252	23	1138	85	456
Bristlecone pine	959	44	803	18585	0	2284	0	69
Mixed Conifer	347	55	10907	237	8	1227	73	152
Ponderosa pine	0	0	0	0	337	852	564	371
Spruce-fir	698	10	579	145	0	2558	72	273

Table 2.9. This table compares the Peaks tree diameters from 1876 with Leiberg's study in 1896. For PIEN, PIPO, and PSME, these are average diameters. For ABLA and PIAR, these are the diameters of the largest trees. Unfortunately, data were not directly comparable. In Leiberg's study, diameter was taken two feet above the ground. Our data is reconstructed at DBH. In only some cases does Leiberg give actual values, and in many cases they are estimates (such as PIAR). However, the data are somewhat similar. In most cases, our values are lower, which make sense taken higher up the boles.

	ABLA	PIAR	PIEN	PIFL	PIPO	POTR	PSME
1876	35.7 cm	40.5 cm	29.1 cm	31.0 cm	40.8 cm	29.8 cm	48.7 cm
Leiberg	frequently 25 cm	rarely exceeds 51-61 cm	25-40 cm	No data	46 cm	No data	56 cm

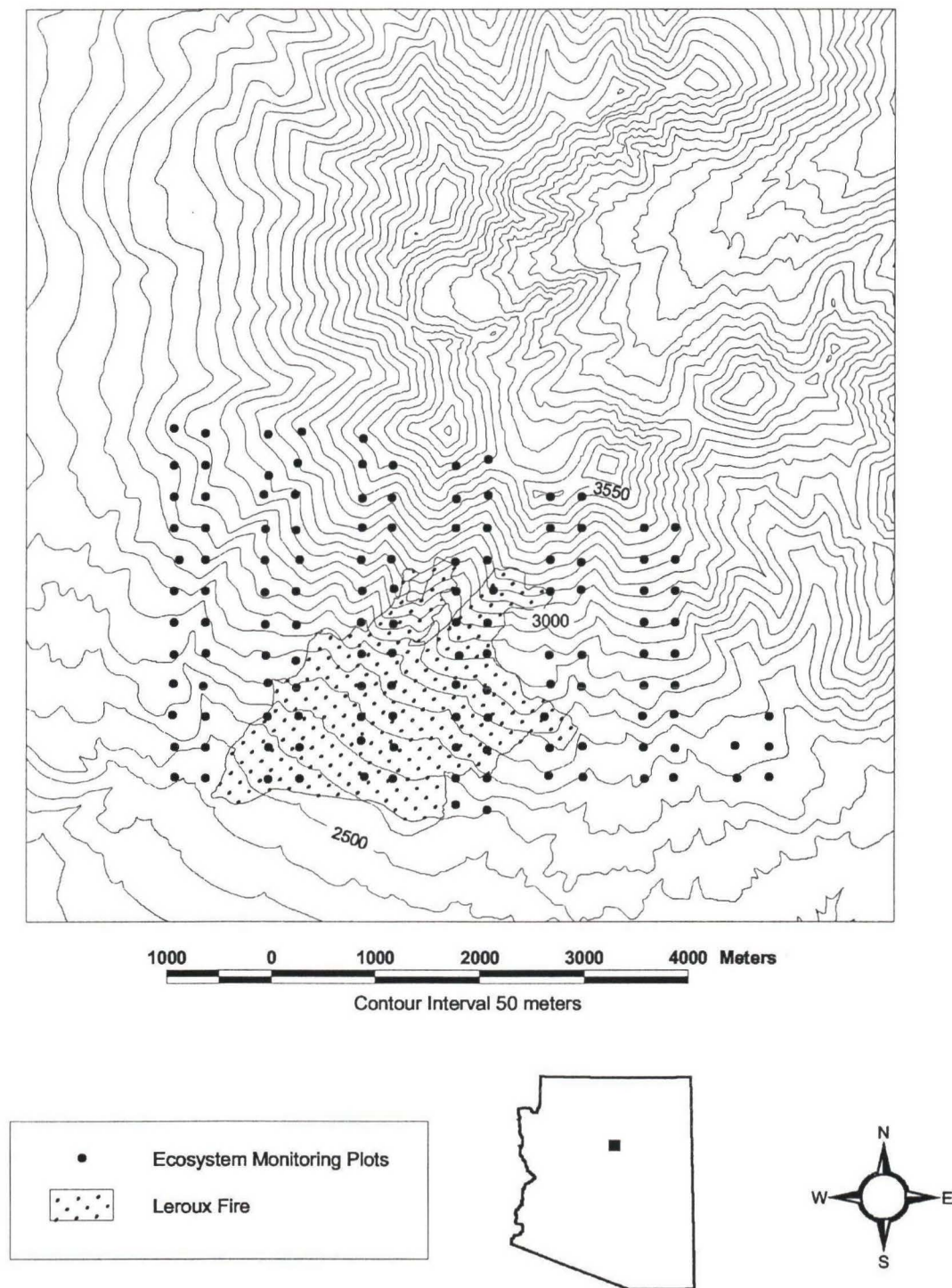


Figure 2.1. Elevational gradient with 135 sample plots on the San Francisco Peaks, northern Arizona. The Leroux fire (shaded) burned in 2001.

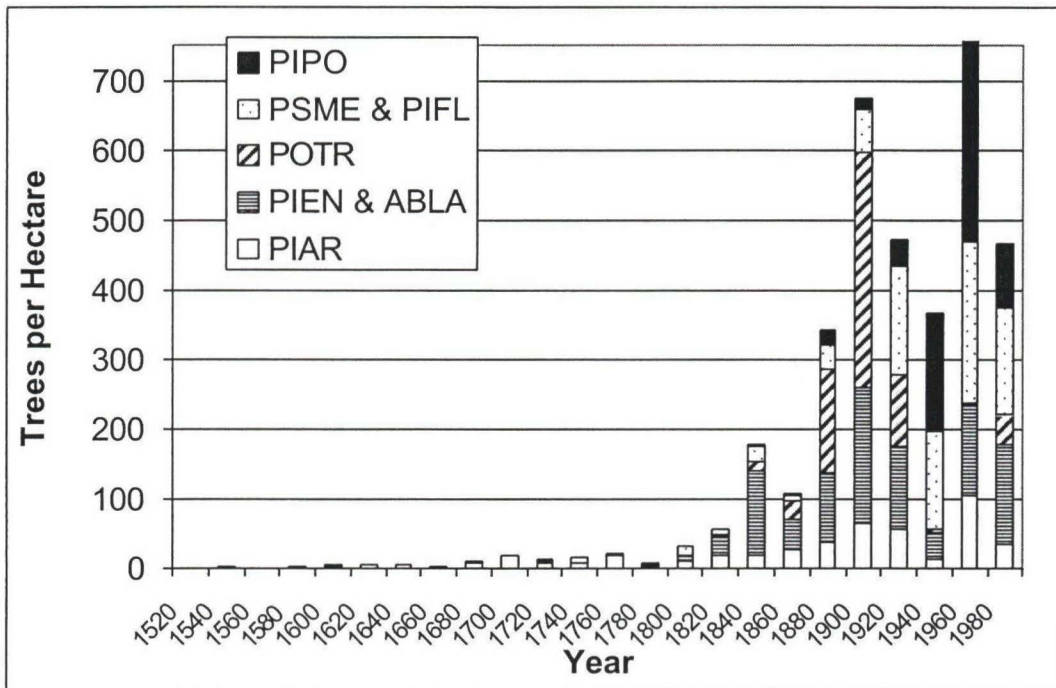


Figure 2.2. Age distributions in 20-year intervals of trees = 2.5 cm diameter on an elevational gradient on the San Francisco Peaks, Arizona.

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Chapter 3: Changes in Forest Vegetation and Arbuscular Mycorrhizae Along a Steep Elevational Gradient in Arizona

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Introduction

Elevation gradients are important drivers of plant community associations. Merriam (1890) pointed out the similarities between high latitude and high altitude plant communities. His “life zones” concept implicitly agreed with the theory, later championed by Clements (1916), of communities as discrete units. Gleason (1926) argued for individualistic plant associations by pointing out that transition zones between vegetation types are wider where elevation gradients are more gradual. Neither Gleason’s nor Clements’s theories completely describe community distributions, but current theory retains elements from both (Shipley and Keddy, 1987; Callaway, 1997). Numerous studies of elevation gradients, such as those in the United States’ Santa Catalina and Great Smoky Mountains and Israel’s Mount Hermon, supported Gleason’s argument by finding little overlap in plant species distributions (Whittaker, 1965; Whittaker and Niering, 1968; Auerbach and Shimda, 1993; Sagers and Lyon, 1997). However, dominant species may affect community composition by modifying the local environment (Collins *et al.*, 1993; Hoagland and Collins, 1997). Furthermore, species can affect the distributions of other species even if their distributions are non-overlapping (Callaway, 1997; Callaway and Walker, 1997). A global study on plant interactions along elevation gradients found interactions between plants change from competition to facilitation as abiotic stress increases (Choler *et al.*, 2001; Callaway *et al.*, 2002). These findings emphasize the importance of interactions between biotic as well as abiotic factors in determining species distributions (Callaway, 1997; Choler *et al.*, 2001; Callaway *et al.*, 2002).

The San Francisco Peaks in Arizona is a particularly good area to study vegetation distributions because it contains representatives of all southwestern forest types arrayed along a steep elevation gradient. Ponderosa pine, the most common forest type in northern Arizona and New Mexico, is found in the lowest elevations (Brown, 1994). Higher elevation forest types are infrequent in the Southwest (Brown, 1994). On the San Francisco Peaks they are thought to be a remnant population of a colder glacial period that have become isolated due to glacial retreat (Schaack, 1983; Brown, 1994). Above ponderosa pine forest, there is mixed conifer forest, dominated by Douglas-fir and limber pine, then aspen stands, spruce/fir forest, and bristlecone pine forest. Rocky Mountain bristlecone pine trees are found only in the highest elevations of Arizona, Colorado, and New Mexico (Brunstein and Yamaguchi, 1992). The San Francisco Peaks culminate in the only tundra vegetation in Arizona (Rominger and Paulik, 1983; Schaack, 1983; Brown, 1994).

Changes in disturbance regimes across elevation have an important influence on plant communities (Harmon *et al.*, 1983). Prior to settlement by Euro-Americans, fire was a frequent disturbance in the ponderosa pine forests of the southwestern United States; its exclusion is theorized to have caused dramatic changes including decreases in herbaceous production and decomposition rates and increases in tree density and fuel loads (Covington and Moore, 1994; Fulé *et al.*, 1997). Landscape biodiversity and abundance of native plants adapted to low-intensity fire may decline without fire disturbance (Keane *et al.*, 2002; Beier and Maschinski, 2003; Korb and

Springer, 2003). Fire exclusion is also a factor in decreasing aspen forests on the San Francisco Peaks and across the west, as old aspen stands become replaced by conifers (Kay, 1997; Turner *et al.*, 2003; Cocke, 2004). Forest stand structure indicates higher elevation forests have a longer fire regime and thus have been less disrupted by fire exclusion (Cocke, 2004).

The unique forests of the San Francisco Peaks may be particularly susceptible to climate change because climate change is expected to have the most dramatic effects in boreal forests (Hansen *et al.*, 2001; Malcolm *et al.*, 2002). Migration rates required for spruce/fir forest could exceed by a factor of ten the fastest migration rates ever noted in the past (Malcolm *et al.*, 2002). For boreal forest on the San Francisco Peaks, northward migration would require moving across areas currently occupied by Great Basin desert grassland. This is of particular concern with bristlecone pine forests because they are globally rare and no analogous pine-dominated forests exist in high latitudes.

Some of the most dramatic effects of climate change may come through alterations in fire regimes (Flannigan *et al.*, 2000; Dale *et al.*, 2001). Failing to incorporate altered fire regimes in projections of future climate change can decrease our ability to make accurate predictions (Korb and Ranker, 2001). The increased intensity of fires burning in heavy contemporary fuels can also facilitate invasion by exotic species (D'Antonio, 2000). Fire increases invasibility by removing perennial vegetation, canopy cover and soil organic matter, all of which make unused resources available to invaders (Whelan, 1995; Davis *et al.*, 2000; Keane *et al.*, 2002). Fire has already been shown to increase exotic species richness and abundance in this area (Crawford *et al.*, 2001; Griffiths *et al.*, 2001).

Many gradient studies are limited because they compare plant communities solely to changes in the abiotic environment (Callaway, 1997), overlooking the role of arbuscular mycorrhizal fungi (AM). Arbuscular mycorrhizal fungi form associations with plants that range from mutualistic to parasitic and affect plant fitness and competitive interactions (Allen and Allen, 1990; Johnson *et al.*, 1997; Wilson and Hartnett, 1998; Hart *et al.*, 2003). Almost all vascular plant species, with the notable exception of coniferous trees, can function as hosts for arbuscular mycorrhizae (Mosse *et al.*, 1981). AM are commonly known to assist host plants with phosphorous uptake, but may also provide other benefits including protection from fungal pathogens, assisting with the uptake of other nutrients such as nitrogen and copper, and improving water relations (Newsham *et al.*, 1995). In return, AM fungi receive photosynthetic products from the host plant.

There is abundant evidence that AM fungi influence plant species composition and richness in grasslands (Grime *et al.*, 1987; Gange *et al.*, 1993; Wilson and Hartnett, 1997; Hartnett and Wilson, 1999). These studies have compared plants grown in the presence of AM fungi to the absence of AM fungi. However, AM fungi are thought to be ubiquitous in undisturbed grassland soils (Allen *et al.*, 1995), therefore changes in AM species composition probably have greater ecological relevance in grasslands than AM presence alone (van der Heijden *et al.*, 1998a; van der Heijden *et al.*, 1998b; Hart *et al.*, 2003; Klironomos, 2003). In coniferous forests, where the trees form associations almost exclusively with ectomycorrhizae, differences in AM inoculum could be more dramatic (Trappe, 1962; Ahlenslager, 1987; Benjamin *et al.*, 1989). Although there are few studies of AM fungi in coniferous forest ecosystems, all have found decreasing colonization with increasing live tree cover (Kovacic *et al.*, 1984; Gildar, 2002; Korb *et al.*, 2003b). Furthermore AM fungi are absent from high latitudes and AM colonization is low near alpine summits (Read and Haselwandter, 1981; Bledsoe *et al.*, 1990). If the presence of AM fungi alters the competitive balance between understory plants in coniferous forest, ecological implications could include

changing the speed of plant community shifts under climate change scenarios or modifying the forage value of vegetation (McNaughton and Oesterheld, 1990; Perry *et al.*, 1990).

In this study we assessed the herbaceous vegetation and AM inoculum potential on the San Francisco Peaks, crossing a steep, south-facing elevational gradient. We expected that: 1) the species composition, richness, and abundance of the understory vegetation would differ between forest types covering different elevational bands. Species richness was expected to decline with elevation, with the lowest species richness in bristlecone pine forest, except aspen vegetation was expected to have the highest species richness and species abundance. 2) Exotic plants were expected to be distributed in accordance with two hypotheses: first, communities with fewer natives would be the most heavily invaded; second, exotics would dominate where disturbance was more prevalent. Due to past management and modern recreation, there was more disturbance at the bottom of the San Francisco Peaks, so lower elevations were expected to have greater richness and abundance of exotic species. 3) AM inoculum potential was expected to decrease with increases in tree cover. AM inoculum potential was expected to decrease with increasing elevation, possibly disappearing in the highest elevations.

Study Area

We conducted our study on the south face of the San Francisco Peaks within the Coconino National Forest in northern Arizona, centered on lat. 35° 18', long. 111° 41' (Figure 3.1). The San Francisco "Peaks" are actually the caldera of a single extinct volcano. Three peaks around the caldera, Humphreys, Agassiz, and Fremont Peaks, are the highest points in Arizona (3851, 3766, and 3648 m respectively). Because of its volcanic origin, soil parent material is primarily andesite, rhyolite and basalt. Soils are chiefly inceptisols, alfisols, and mollisols (Terrestrial Ecosystems Survey, 1995). A weather station at 2240 m, slightly lower in elevation than our study area, records average annual precipitation of 56 cm. Average July maximum temperature is 27° C and average January minimum temperature is -12° C (Western Regional Climate Center, 2003). Over a 1000 m elevation increase on the San Francisco Peaks, precipitation increases by 11 cm while temperatures decrease by 6.89° C (Pearson, 1920a).

Since Euro-American settlement (circa 1876), the San Francisco Peaks were used for summer grazing of sheep and cattle starting in the 1870's, peaking around 1915 (Cline, 1994). Lower elevation ponderosa pine and mixed conifer forests were logged, though higher elevation forests were excluded from harvest because of the steep terrain. Since the Kachina Peaks Wilderness Area was established in 1984, it has received an increasing number of recreational visitors and a downhill ski area operates on 137 acres on the west side of the mountain (Aitchison, 1989; Grand Canyon Trust, 2000).

Methods

We assessed plant community composition, site conditions, and overstory tree conditions on 121 plots located systematically on a 300 m grid that extended from ponderosa pine forest at 2442 m to timberline at 3569 m (Figure 3.1). We were only examining the understory within the context of a forested overstory, so if a plot origin fell in a meadow or other unforested location, we attempted to relocate the plot 50 m to the N, E, W, or S. If these were also unforested we did not establish the plot.

Plot design was based on the National Park Service's Fire Monitoring protocol (National Park Service, 1992; Fulé *et al.*, 2002a). Appendix 1 shows how each plot was set up and where we

took all samples and measurements. Plots were 20 m x 50 m (1000 m²), with the longer axis oriented uphill to capture the elevation gradient and enable correction of the plot area for slope. Plot corners and center were permanently marked with iron stakes placed flush to the forest floor. We recorded the distance and direction from a tagged reference tree to the plot center and recorded GPS coordinates, slope, azimuth and elevation of the plot.

Each plot was measured once between the years 2000 and 2003. Sampling took four years because plots all had to be reached on foot, forests were closed to research in 2000 and 2002 due to extreme drought, and a wildfire in 2001 also closed the forest for several weeks. We do not believe the year a plot was sampled had a significant effect on our results. First, representatives of all five forest types were sampled in 2000, 2001 and 2003. This meant that between year sampling did not duplicate the results between forest types. In 2002, only three plots were sampled, all of which were bristlecone pine forest. This is a small proportion of the 21 bristlecone pine plots, and therefore should not sway the results. Although climatic conditions differed between sampling years, all years were somewhat similar in that precipitation was below average. Finally, independent samples T-tests did not detect differences in species richness or composition between sampling years.

All trees on the 1000 m² plot with a diameter at breast height (dbh) greater than 15 cm were measured; trees with dbh 2.5 to 15 cm were measured on a 250 m² subplot and trees < 2.5 cm dbh were measured on a 50 m² subplot. For each tree we recorded dbh, crown base height, total height, damage and decay class of snags (Thomas *et al.*, 1979).

Herbaceous plant abundance was measured on two point-line intercept transects per plot, running along the 50 m plot boundaries. Every 30 cm we recorded all species encountered, height of the tallest species, and underlying substrate (litter, rock, etc.). To calculate plant abundance, we divided the number of plants encountered on each point-line intercept transect by 332, the total number of points sampled per plot. Since more than one plant could be encountered at a single point, it was possible for plant abundance to exceed one. Every three m we measured tree canopy cover by vertical projection. We recorded presence/absence of all vascular plant species on a belt transect (10 X 50 m) centered on each point-line intercept transect.

Soil samples were collected in 2002 for measuring AM fungal inoculum potential on 75 of the 121 plots. We chose plots that were established no later than 2002, were not burned in a 2001 wildfire that covered part of the study area, were located on (Figure 3.1). Soil sampling plots ranged in elevation from 2442 m to 3559 m, only 10 m less than the elevation range for the full study area.

Plant species can have significant effects on the fungal communities beneath them (Bever *et al.*, 1996; Eom *et al.*, 2000). Therefore, we chose to sample under grasses, rather than at random points on the plot, to confirm that any mycorrhizal differences we encountered were not an artifact of changes in the presence or abundance of certain species. We recorded the grass species under which the sample was taken. We collected soil by clearing away the organic layer, then pounding a 3.8 cm diameter pipe 15 cm into the ground. We took two soil cores from underneath the clump of grass closest to the center of each point-line intercept transect.

Roots from one of each of the paired soil samples were elutriated, dried, and weighed to estimate the root biomass available as a mycorrhizal inoculant. The other paired soil sample was transported to the lab in the soil corer for a corn bioassay to determine mycorrhizal inoculum potential (Johnson *et al.*, 1999). The purpose of using an intact soil core was to retain root and AM

hyphal networks substantially intact (Klironomos and Hart, 2002). We covered the bottom of the corer with shade cloth to prevent soil loss but allow water drainage, and then planted a germinated corn seedling (*Zea mays*) in the soil core. After six weeks, we harvested the corn plants. To assess percent colonization by AM fungi, we harvested, stained, and scored the roots using the grid-line intersect method (Johnson *et al.*, 1999).

To test for greenhouse contamination, we planted corn seedlings in steam-sterilized soil in five additional cores. AM colonization in the controls ranged between 0% and 5.5% (mean $2.8\% \pm 1.0$). Therefore only about 2 – 4% of the colonization we observed could be due to greenhouse contamination. All control plants were entirely free of non-AM fungi.

Data Analysis

We categorized each plot into one of five forest types based on an importance value for each tree species calculated from the sum of the relative frequency (percent stems) and relative abundance (percent basal area) (Taylor, 2000; Fué *et al.*, 2003). If the highest importance value on a given plot was *Pinus ponderosa*, *Populus tremuloides*, or *Pinus aristata*, we assigned it to the ponderosa pine, aspen, or bristlecone pine forest type, respectively. If the highest importance value was for *Pinus flexilis* or *Pseudotsuga menziesii* (limber pine or Douglas-fir), we assigned it to the mixed conifer forest type. If the highest importance value was for *Abies lasiocarpa* var. *arizonica* or *Picea engelmannii* (corkbark fir or Englemann spruce) we assigned it to the spruce/fir forest type. Henceforth in this paper, the scientific names are used to refer to individual tree species, while common names are used to refer to forest types (e.g., “ponderosa pine forest” or “spruce/fir forest”).

Due to the long sampling period and difficult access, it was not possible to conduct all the plant measurements under ideal phenological conditions. Some understory plants were difficult to identify in the field, so it was necessary to group certain taxa by genus for analysis (e.g., *Bromus anomalus* and *Bromus ciliatus* were called *Bromus* spp.). For this reason, species richness and species diversity measures are underestimates. Appendix 2 is a summary of the groupings we made for analysis purposes.

Total plant abundance, exotic plant abundance, abundances of individual species and groups of species, and species diversity (Shannon's H') were calculated from point-line intercept data. We used the data from the belt transect to calculate species richness.

Multivariate community analyses were carried out with PC-Ord software (McCune and Mefford, 1999). We used Nonmetric Multidimensional Scaling (NMDS) to visualize differences in plant community composition. In NMDS analyses, we used Sorenson distance with a random starting configuration and 40 runs with real data. We used 50 runs with randomized data in the Monte Carlo test. We choose the highest dimensionality that yielded a final stress lower than 95%. We decided our solution was sufficiently stable when we reached an instability < 0.0001 or 500 iterations.

Differences in community composition were tested with Multi-response Permutation Procedures (MRPP). MRPP creates a distance matrix between group members, then compares the within group distances and the between group distances of random permutations to the actual groups. MRPP output is composed of a p-value and the chance-corrected within-group agreement (A), a measure of effect size. Our MRPP analyses were done using Euclidean distance.

Indicator species analysis was used to identify species that were particularly faithful and/or exclusive to individual forest types (McCune and Grace, 2002). A comparison between the maximum indicator value of a species (ranging between 0 – 100) and randomized trials for the occurrence of that species (1000 randomizations in the Monte Carlo test) yields a p-value. To be a perfect indicator value, a species would need to be found on all plots in a forest type and not found on any plots of any other forest types. We accepted species with indicator values = 25 and p-values = 0.05 as indicator species.

We used Mantel tests to find correlations between different sets of data taken on the same set of plots. The output from a Mantel test is a standardized Mantel statistic (r) that indicates the strength of the correlation between the distance matrices of the two data sets and a p-value. We chose Mantel's asymptotic approximation to evaluate test statistics.

SPSS software (2002) was used for parametric and nonparametric univariate analyses. All variables used in parametric tests were checked for normality and equal variance by confirming the Shapiro-Wilk's and Levene's test statistics were both > 0.05 . Statistically significant differences between sampled populations were assessed with t-tests or ANOVA. Alpha level for all tests of statistical significance was 0.05. Individual means were compared following significant ANOVAs using Tukey's HSD post hoc test. Variables that did not meet the assumptions for parametric statistics were assessed with nonparametric methods of analysis. ANOVA's were replaced with Kruskal-Wallis tests and t-tests were replaced with Wilcoxon Signed Ranks tests. We used Pearson's correlations to look for relationships between factors.

Results

Vegetation Distribution

The sampling grid included 26 ponderosa pine, 27 mixed conifer, 37 aspen, 10 spruce/fir and 21 bristlecone pine plots (Table 3.1). In a companion study, Cocks (2004) showed that the sampling grid was representative of the actual proportions of each forest type in the study area, as measured by classified satellite imagery. Plant community composition differed between the five forest types (MRPP, $A = 0.08$, $p < 0.01$). Mixed conifer and aspen appeared to have the most similar community composition (Figure 3.2). The vegetation types at opposite ends of the elevational gradient, ponderosa pine and bristlecone pine, shared traits of high species richness and low canopy cover. Plant community composition was correlated with the environmental variables canopy cover, elevation, exotic species richness, plant abundance, slope, Shannon's H' diversity index, species richness, and forest type (Mantel test, $r = 0.54$, $p < 0.01$).

Forest types were differentiated both by species richness (ANOVA, $F_{(4, 116)} = 7.29$, $p < 0.01$) and canopy cover (ANOVA, $F_{(4, 116)} = 11.749$, $p < 0.01$) (Table 3.1). Shannon's H' diversity index did not vary between vegetation types. Canopy cover and species richness were inversely related ($r = -0.48$, $p < 0.01$). Species richness in ponderosa pine forest (average 32.6 species/1000 m^2 plot) was significantly higher than all forest types except bristlecone pine. Bristlecone pine and ponderosa pine, the two forest types with least canopy cover, differed from the two forest types with greatest cover, aspen and mixed conifer.

Plant abundance also varied between forest types (Kruskal-Wallis, $\chi^2_{(4)} = 29.46$, $p < 0.01$) and was not correlated with richness. Plant abundance was 36% higher in aspen than in ponderosa pine, the forest type with the next highest plant abundance. *Populus tremuloides* was the only tree species whose basal area was positively associated with plant abundance ($r = 0.49$, $p < 0.01$).

Nitrogen fixing plants were more abundant on plots with high *P. tremuloides* basal area (N fixers $r = 0.72$, $p < 0.01$).

Pinus ponderosa basal area and plant abundance were negatively related ($r = -0.23$, $p = 0.01$). In particular, high *P. ponderosa* basal area was associated with low abundances of nitrogen fixing plants and shrubs (N fixers $r = -0.32$, $p < 0.01$; shrub $r = -0.22$, $p = 0.01$). Plant abundance was inversely related to basal area of *Pseudotsuga menziesii* and both tree species associated with spruce/fir forest (*P. menziesii* $r = -0.24$, $p = 0.01$; *Picea engelmannii* $r = -0.24$, $p = 0.01$; *A. lasiocarpa* $r = -0.22$, $p = 0.02$). *Pinus aristata* was the only species to be significantly positively associated with shrub abundance ($r = 0.55$, $p < 0.01$).

Fourteen indicator species were identified for ponderosa pine forest, four for mixed conifer, none for aspen, two for spruce/fir, and eight for bristlecone pine forest (Table 3.2). Abundances of all three grasses that were ponderosa pine indicator species were positively correlated with species richness (*M. montana* $r = 0.54$, $p < 0.01$; *E. elymoides* $r = 0.36$, $p < 0.01$; *F. arizonica* $r = 0.35$, $p < 0.01$). There were also positive correlations between the abundances of ponderosa pine indicator species and species richness of N-fixing plants (*E. elymoides* $r = 0.52$, $p < 0.01$; *F. arizonica* $r = 0.47$, $p < 0.01$; *M. montana* $r = 0.45$, $p < 0.01$; *Lupinus* spp. $r = 0.25$, $p < 0.01$). Of the mixed conifer indicator species, *Mahonia repens* was associated with plots that had high canopy cover ($r = 0.23$, $p = 0.01$). Two bristlecone pine indicator species were more abundant on plots with high species richness (*Festuca ovina* $r = 0.21$, $p = 0.02$; *Erigeron* spp. $r = 0.21$, $p = 0.02$). There was an inverse relationship between the abundances of bristlecone pine indicator species and richness of nitrogen fixing species (*Ribes montigenum* $r = -0.33$, $p < 0.01$; *Penstemon whippleanus* $r = -0.33$, $p < 0.01$; *Festuca ovina* $r = -0.27$, $p < 0.01$). *Penstemon whippleanus* abundance was correlated with the percent cover of soil ($r = 0.21$, $p = 0.02$).

Exotic Species

Native plant community composition on plots with exotic species differed from native plant composition on plots without exotics (MRPP, $A = 0.01$, $p < 0.01$). Plots with exotic species tended to be those with low canopy cover and high species richness (Figure 3.3). Exotic species richness differed between forest types (Kruskal-Wallis $\chi^2_{(4)} = 9.84$, $p = 0.04$). Mean exotic species richness was nearly twice as high in ponderosa pine as in bristlecone pine and aspen forests, which had the next highest exotic species richness (Table 3.1). Exotic species richness was positively correlated with both native species richness and native plant abundance (native richness $r = 0.46$, $p < 0.01$; native abundance $r = 0.41$, $p < 0.01$). However, exotic species richness was inversely related to canopy cover and elevation (canopy $r = -0.39$, $p < 0.01$; elevation $r = -0.19$, $p = 0.04$).

Abundance of exotic species showed similar trends to exotic species richness and the two variables were positively correlated ($r = 0.58$, $p < 0.01$). Exotic plant abundance was positively correlated with native plant abundance and native species richness (native abundance $r = 0.54$, $p < 0.01$; native richness $r = 0.20$, $p = 0.03$). Exotic plant abundance also decreased with increasing canopy cover ($r = -0.18$, $p = 0.05$). Exotics accounted for no more than 6% of plant encounters on any given plot.

Of the 200 different species encountered in this study there were 11 exotic species, 187 native species, and two which we could only identify to genus making us uncertain of their origin. A full species list is given in Appendix 2. The exotic species were *Bromus inermis*, *B. tectorum*, *Dactylis glomerata*, *Lactuca serriola*, *Linaria dalmatica*, *Poa compressa*, *P. pratensis*, *Sanguisorba minor*, *Taraxacum officinale*, *Tragopogon dubius*, and *Verbascum thapsus*. We also

found a *Chenopodium* that may be the exotic *C. album* or the native *C. berlandieri*. We counted this *Chenopodium* as a native species in our analysis.

The patterns of distribution of individual exotic species varied with elevation (Figure 3.4). *Taraxacum officinale* was the only exotic species we encountered frequently enough (37% of belts) to analyze its individual abundance. *T. officinale* was more abundant on plots high in abundance of both exotic and native species (exotic abundance $r = 0.56$, $p < 0.01$; native abundance $r = 0.33$, $p < 0.01$) and was positively correlated with exotic species richness and native species richness (exotic richness $r = 0.58$, $p < 0.01$; native richness $r = 0.32$, $p < 0.01$). Plots with little canopy cover also had more *T. officinale* ($r = -0.24$, $p = 0.01$). *T. officinale* was the most common (or only) exotic species in the higher elevation sites (Figure 3.4). Excluding *T. officinale* from exotic species richness resulted in a larger negative correlation with elevation (excluding *T. officinale* $r = -0.34$, $p < 0.01$; including *T. officinale* $r = -0.19$, $p = 0.04$).

Nine native species were indicators for plots with exotic species and six native species indicated plots without exotics (Table 3.3). Abundance of indicator species for plots with exotic species was positively correlated with native species richness and abundance as well as exotic species richness and abundance (Table 3.4).

Arbuscular Mycorrhizal Colonization

A total of 135 soil samples were collected: 14 in ponderosa pine, 33 in mixed conifer, 59 in aspen, 10 in spruce/fir, and 19 in bristlecone pine forest. We sampled soil under eight species of plants: *Blepharoneuron tricholepis*, *Bromus* spp., *Elymus elymoides*, *Festuca arizonica*, *Muhlenbergia montana*, *M. virescens*, *Pascopyrum smithii*, and *Poa fendleriana*. Only two samples were collected under *Pascopyrum smithii* and three under *Blepharoneuron tricholepis*. This was insufficient to provide an adequate idea of the variation within those species, so they were not included in the analysis by species.

Plots with high understory plant abundance had higher AM fungal colonization (Table 3.1), although this accounted for only a small amount of the variability (regression, $F_{(1, 134)} = 4.87$, $p = 0.03$, $r^2 = 0.04$). Percentage AM fungal colonization was positively associated with high species richness and low basal area (species richness $r = 0.18$, $p = 0.04$; basal area $r = -0.20$, $p = 0.02$). Neither the richness nor abundance of exotic species was related to AM colonization. AM fungal colonization and non-AM fungal colonization were also positively correlated ($r = 0.40$, $p < 0.01$). Root biomass available as inoculant was not related to percent AM colonization.

AM colonization differed based on the grass it was collected under (ANOVA $F_{(5, 124)} = 2.90$, $p = 0.02$). AM colonization was highest in corn plants grown in soil from under *Muhlenbergia virescens* ($38.4\% \pm 11.8$). This was 240% higher than AM colonization of corn grown in *Bromus* spp. soil ($16.1\% \pm 1.9$) and 300% higher than corn grown in *Poa fendleriana* soil ($12.8\% \pm 2.5$).

Bromus spp., *M. montana*, and *F. arizonica* were the only three grass species under which we collected more than ten soil samples (23, 39, and 49 samples, respectively). Soil samples from under each of these species spanned an elevation range greater than 850 m and were occurred in all five forest types. In soil collected under *M. montana*, AM colonization increased with elevation (regression, $F_{(1, 37)} = 7.37$, $p = 0.01$, $r^2 = 0.17$). AM colonization did not change with elevation from soil collected under *Bromus* spp., *F. arizonica*, or when soil samples were not separated by grass species.

Discussion

Plant Community Differences

Our hypothesis that species richness would differ between forest types was supported, although it did not follow the pattern that we expected. Brown (1994) claimed that the richness of the aspen understory is an important wildlife resource; therefore, we expected that aspen forest would have the highest species richness. We also expected an overall decrease in species richness with elevation. Instead we found that aspen forest had the lowest species richness and species richness was low in the middle elevations and high in ponderosa and bristlecone pine forest, the highest and lowest elevation forests. Low canopy cover in bristlecone and ponderosa pine forest may explain the high species richness as there was a negative correlation between species richness and canopy cover overall. Landscape variation created by frequent low-severity burns creates diverse habitats (Keane *et al.*, 2002). This may account for high species richness in ponderosa pine forest, although bristlecone pine has not been noted for a frequent fire regime. In 1876, 15% of the current ponderosa pine forest plots were substantially unforested with total tree basal areas less than 3 m²/ha. The current high species richness in ponderosa pine forest may be a relict from when these plots were less forested. However, there have also been substantial increases in the basal area of current aspen plots over the past century, and aspen plots had the lowest species richness (Cocke, 2004).

The pattern of high species richness in the low and high elevation forest, with lower species richness in the middle elevations was also reported by Allen *et al.* (1991) in the southern Rocky Mountains. Although the plot size in their study was similar to ours, their overall species richness was between 5% and 65% larger than what we are reporting for the San Francisco Peaks. The isolation of the high elevation forest on the San Francisco Peaks may explain the discrepancy. However, Allen *et al.* (1991) also reported a positive correlation between species richness and site moisture. Average yearly precipitation in northern Arizona (56 cm) is similar to that at their wettest site (Rocky Mountain National Park, 53 cm). However, we sampled during 2000 – 2003, when precipitation throughout the Southwest averaged 5.1 cm/year below normal (Lawrimore, 2004). Allen *et al.* (1991) sampled during 1985 – 1986, when precipitation was 5.8 and 8.0 cm above normal, respectively (Lawrimore, 2004). The drought may have resulted in low species richness in our study area, as it has in other parts of the Southwest (Fulé *et al.*, 2002b).

Although we found differences in species richness, we did not find differences in Shannon's H' diversity index. Shannon's H' accounts for how evenly abundance is distributed among species as well the number of species present (Magurran, 1988). The lack of difference in Shannon's H' may indicate abundance was more evenly distributed among all species in the plots with low species richness. Alternatively, methodological problems may have obscured differences in diversity between forest types. The point-line intercept method tends to underestimate species richness and overestimate cover, compared to quadrat methods (Korb *et al.*, 2003a). As a consequence, any species diversity index calculated from point-line intercept data should be low. We believe comparisons based on the point-line intercept method are still valuable because this was a systematic error that has similar effects on all plots within our study area. Therefore comparisons of both species diversity and cover should still reflect differences between forest types.

We confirmed our hypothesis that plant abundance differed between forest types and was highest in aspen forest. Abundance of herbaceous plants could be higher in aspen forest because the nutrient content of leaves, rather than conifer needles, alters soil nutrient and pH conditions

(Fisher and Binkley, 2000). Alternatively, the extra light available in the spring before aspen leaves emerge could be important to understory plants.

Species composition differed between forest types with ecological links between indicator species and historical patterns of disturbance regime and forest structure. Our results agree with Naumburg and DeWald (1999) who found species composition was related to the disturbance history of the plot.

Ponderosa pine forests are adapted to a fire regime of frequent low intensity fire, associated with historically open, grassy stands (Cooper, 1960; Swetnam and Baisan, 2003). *Astragalus rusbyi*, *Ceanothus fendleri*, *Cirsium* spp., *Elymus elymoides*, *Lupinus* spp., *Muhlenbergia montana*, and *Verbascum thapsus*, all indicator species for ponderosa pine forest, are well-adapted to surviving or recolonizing after fire (Walsh, 1995; Simonin, 2001; Beier and Maschinski, 2003; Hull-Sieg *et al.*, 2003; Korb and Springer, 2003). Four ponderosa pine indicators, *Antennaria parviflora*, *Elymus elymoides*, *Festuca arizonica* and *Muhlenbergia montana*, grow poorly in shaded conditions (Matthews, 1993; Walsh, 1995; Naumburg and DeWald, 1999; Naumburg *et al.*, 2001; Simonin, 2001). Ponderosa pine was also characterized by a diversity of nitrogen fixing species, although not an abundance of them. Six of the fourteen ponderosa pine indicator species were nitrogen fixers (*Astragalus humistratus*, *A. rusbyi*, *Ceanothus fendleri*, *Lotus* spp., *Lupinus* spp., and *Oxytropis lambertii*). Both NH_4^+ and NO_3^- are lower in ponderosa pine forests than most other forest types and may be more limiting than in other forest types (Stark and Hart, 1997).

Despite ponderosa pine and mixed conifer forest being near each other in elevation and similar in historical fire regime (Heinlein, 1996; Fulé *et al.*, 2003), there was little overlap in species composition between the two forest types (Figure 3.2). Three of the four mixed conifer indicator species are adapted to surviving either with or without fire. *Holodiscus dumosus* colonizes disturbed and burned areas well, but is also considered indicative of late seral communities (McMurray, 1987). *Mahonia repens* can survive fire and exists in both shade and full sun, although in our study it was encountered more frequently in more shaded areas (Walkup, 1991). *Pteridium aquilinum* requires fire for regeneration by spores, but more often regenerates vegetatively (Crane, 1990).

We found no indicator species for aspen forest. However, there were correlations between *Populus tremuloides* and abundance of nitrogen fixing plants. In particular, two legumes, *Lathyrus lanszwertii* var. *leucanthus* and *Lathyrus* or *Vicia* spp., were between 2 and 25 times more abundant on aspen plots than in other forest types. However, both species were found on 85% of all plots and one or both of them were among the most common species encountered in all five forest types (Table 3.1). We used the presence or absence of species to determine indicator species, therefore a species that is present in a variety of forest types, but notably abundant in one, would not emerge in the analysis.

Basal area in spruce/fir forest is more than 20% greater than any other forest type on the San Francisco Peaks (Cocke, 2004). The two indicators for spruce/fir forest are both genera commonly associated with moist, shady areas. Neither indicator species disperses widely, consistent with a stand-replacing fire regime in spruce/fir (McLachlan and Bazely, 2001). The widest variation in species composition occurred in spruce/fir forest (Figure 3.2). This may be because of variation in species composition between the dense stands of trees that characterize spruce/fir forest, and unforested openings where most herbaceous species are concentrated (Brown, 1994).

We were surprised by the number of shared characteristics between bristlecone pine forest and ponderosa pine forest. Some bristlecone pine plots were more similar to ponderosa pine plots than spruce/fir plots; even though mean elevation in spruce/fir and bristlecone pine forest differs by only 84 m (Figure 3.2). Bristlecone and ponderosa pine forests were high in species richness and low in canopy cover. Mean species richness in these two forest types was 30.9 ± 0.9 , compared to 25.0 ± 0.8 in all other forest types. Canopy cover for bristlecone and ponderosa pine forest was $45.9\% \pm 2.9$, but $66.3\% \pm 1.9$ in all other forest types. They were also the only forest types that had grasses as indicator species (*Festuca ovina* for bristlecone pine; *Elymus elymoides*, *F. arizonica*, and *Muhlenbergia montana* for ponderosa pine). Germination of one bristlecone pine indicator, *Ribes montigenum*, is thought to be enhanced by low-intensity fire (Marshall, 1995). Bristlecone pine forest differed from ponderosa pine forest in having a high density of shrubs and low richness of N-fixing species. Soil cover was seven times greater in bristlecone pine forest than in any other forest type. One bristlecone pine indicator, *Penstemon whippleanus*, was associated with a high occurrence of bare soil.

Bristlecone pine indicator species on the San Francisco Peaks were similar to species associated with *Pinus aristata* in the Rocky Mountains. Both *Penstemon whippleanus* and *Festuca ovina* were common in one of the six bristlecone pine associations identified by Ranne *et al.* (1997) and *Ribes montigenum* was common in two. In addition, both studies found species of *Erigeron* and *Mertensia* were indicative of bristlecone pine forest.

Exotics and Susceptibility to Invasion

The most invaded communities were the ones with the highest native species richness and abundance, contradicting our hypothesis. This was supported by univariate correlations, multivariate ordinations and correlations between indicator species for plots with exotic species with native species richness and abundance (Table 3.4). Theory, supported by greenhouse experiments, predicts that high biodiversity areas should more completely use available resources, making them more resistant to invasion by new species (Naeem *et al.*, 2000). However, observational studies often show greater richness or abundance of exotic species in areas with higher native species richness (Stohlgren *et al.*, 1999; Stohlgren *et al.*, 2001). Site characteristics, such as water availability and soil fertility, usually vary in observational studies but are held constant in experiments and may account for the discrepancy (Naeem *et al.*, 2000).

Our hypothesis of lower exotic species richness in higher elevations was confirmed although exotic species abundance did not vary with elevation. This suggests exotic species do not face barriers to growth, but may face barriers to dispersal. Roads, campgrounds, and livestock grazing can facilitate invasion by providing a dispersal vector into an area (Knapp, 1996; Allen and Hansen, 1999). However, since the exotic species most frequently encountered in high elevations, *Taraxacum officinale*, has wind dispersed seeds, disturbance should minimally influence its spread.

Alternatively, high-elevation forests on the San Francisco Peaks may have experienced relatively little invasion because seed sources for exotic species well adapted to boreal forest are not available due to the rarity of this forest type in the Southwest. Stohlgren *et al.* (2000) hypothesized low temperatures limited exotic species in the higher elevations of Rocky Mountain National Park. Even though successful invaders often have wide ecological tolerances or can adapt quickly to new conditions (Bazzaz, 1986; Parker *et al.*, 2003), generalist species have ecological limits. Species such as *Bromus tectorum*, *Linaria dalmatica*, and *Verbascum thapsus* that are

known invaders of lower elevation ecosystems may have encountered ecological limitations above ponderosa pine forest (Knapp, 1996; Jacobs and Sheley, 2003; Parker *et al.*, 2003).

Exotic species do not yet appear to be a major portion of the plant community on the San Francisco Peaks. On average, exotic species accounted for only $3.5\% \pm 3.8$ of the total species richness per plot and $0.5\% \pm 1.2$ of the total plant abundance per plot. Exotic species never composed more than 14.3% of the species richness and 6.0% of the abundance. No exotic species were found on 40% of plots and exotic species were not abundant enough to be detected on the point-line transect of an additional 37%. However, plant species composition on plots with exotic species differed from those which had none. Unfortunately, our study design does not allow us to speculate if exotic species change the plant community as whole or if some plant communities are more easily invaded than others.

It is important to identify which exotic species may pose future threats to native vegetation (Parker *et al.*, 1999). We believe *Linaria dalmatica* has the most invasive potential because it is already known to be noxious in this area, responds positively to fire, and seeds are still viable after relatively long-term storage (Jacobs and Sheley, 2003; Zouhar, 2003b). *Verbascum thapsus* is a noxious weed in Arizona and it is frequently encountered in burned areas (Crawford *et al.*, 2001; Hull-Sieg *et al.*, 2003). However, it declines in the absence of recurring soil disturbance (Hull-Sieg *et al.*, 2003). *Taraxacum officinale* has been assumed to be a poor competitor with later seral plants (Esser, 1993). However, our results agree with others who found *T. officinale* is able to invade previously undisturbed areas (Weaver *et al.*, 1990).

Although *Bromus inermis*, *Poa compressa* and *Poa pratensis* are not listed as noxious weeds in Arizona, exotic grasses, such as *P. pratensis*, can be the most commonly encountered exotic species (Weaver *et al.*, 1990; Weaver *et al.*, 2001; Hull-Sieg *et al.*, 2003). In particular, *P. pratensis* was the second most widely distributed exotic species in our study. *Bromus tectorum* has altered many areas of sagebrush steppe so it can no longer support native plant communities (Knapp, 1996; Zouhar, 2003a). *B. tectorum* does not grow well under low-light conditions or under a large organic layer, making it a less severe a threat to forest vegetation (Pierson and Mack, 1990; Pierson *et al.*, 1990). However, it is well adapted to fire and other disturbances (Knapp, 1996; Zouhar, 2003a).

Arbuscular mycorrhizal colonization

Levels of AM inoculum potential that we found are consistent with other studies in coniferous forest. Gildar (2002) and Korb *et al.* (2003b) reported AM inoculum potential in ponderosa pine forest varied between 6 – 24% and 18 – 45%, respectively, depending on the fire history and tree density. Although AM inoculum potential has been assumed low in forests where trees do not associate with AM fungi (Newman and Reddell, 1988), our corn bioassay results report inoculum potentials comparable to those found in other ecosystems. For example, Johnson *et al.* (1991) recorded AM inoculum potential in a prairie varied between 1 – 20%, while Gehring *et al.* (2002) reported AM inoculum potential of between 12 – 19% in a tropical rainforest.

Our hypothesis of negative correlation between AM colonization and basal area was supported, agreeing with findings of researchers in other forest types (Benjamin *et al.*, 1989; Johnson *et al.*, 1991). Benjamin *et al.* (1989) hypothesized AM colonization was low under forest canopy due to inhibition from the ectomycorrhizal fungi colonizing tree roots. Newman and Reddell (1988) used a similar explanation to account for a positive correlation between herbaceous species richness and the abundance of trees capable of associating with AM fungi. If this were

true, we would expect AM infection to be highest in aspen dominated plots because aspen can form associations with both AM and ectomycorrhizae, while most coniferous trees can only form associations with ectomycorrhizae (Trappe, 1962; Mosse *et al.*, 1981; Neville *et al.*, 2002). Our results did not support this theory because AM colonization was no higher in aspen forest than in any other forest type.

Our results that plots with high AM colonization also tended to have high species richness agree with a number of other researchers (Grime *et al.*, 1987; Newman and Reddell, 1988; Moora and Zobel, 1996). However, there were no correlations between AM inoculum and exotic species richness or abundance. In some cases AM fungi may encourage the establishment of native over exotic species (Reeves *et al.*, 1979; Korb, 2001). However, this may vary depending on the specific exotic species in question and the native species with which it interacts (Knapp, 1996; Marler *et al.*, 1999).

Our hypothesis that AM fungal infection would decrease in the highest elevations was not supported. AM infection was highest in bristlecone pine plots, although not significantly so. Changes in AM fungi across landscape gradients are a fertile area of study (Reynolds *et al.*, 2003), but we suspect AM infection levels are affected by microsite differences that were not adequately addressed in a study of this scale. Percent AM colonization varied with the plant the soil was taken under, consistent with the host species effect noted by Eom *et al.* (2000). Canopy cover, tree basal area, soil nutrients, soil moisture, and ecotypes within species also affect the AM community (Anderson *et al.*, 1984; Benjamin *et al.*, 1989; Johnson *et al.*, 1991; Anderson *et al.*, 1994; Schultz *et al.*, 2001). Changes in elevation are necessarily tied with changes in soil moisture, temperature, slope, tree stand structure, vegetation and soil nutrients (Austin, 1999). Important differences in AM inoculum potential may have been lost in these interacting variables. For example, we only found an increase in AM colonization with elevation when we exclusively compared samples collected under *Muhlenbergia montana*. Future studies comparing AM fungi across landscape level gradients would also be improved by examining AM species composition (van der Heijden *et al.*, 1998a; Klironomos, 2003).

Forest Change with Altered Environment

Global surface temperatures are predicted to rise 1-3.5° by the year 2100 (Hanson and Weltzin, 2000). Warming trends are expected to induce migration of communities to higher latitudes or altitudes than they are currently found (Gosz, 1992; Hansen *et al.*, 2001).

The magnitude of climate change will undoubtedly be important to determining whether climate change will increase or decrease the occurrence of a given forest type or species (Whitlock *et al.*, 2003). For example, Baker (1992) concluded *Pinus aristata* establishment was favored by fire, so he predicted that global temperature increases would increase fire frequency, thereby enlarging bristlecone pine forests. A relative of *P. aristata*, Great Basin bristlecone pine or *P. longaeva*, is tolerant of extreme environmental conditions, another trait which should favor these species with the changing climate (Beasley and Klemmedson, 1980). However, *P. aristata* distribution is limited to the top of peaks in Colorado, Arizona, and New Mexico (Brunstein and Yamaguchi, 1992). More extreme temperature changes could decrease the area suitable for their growth (Hansen *et al.*, 2001). As *P. longaeva* and *P. aristata* appear to be poor competitors, their range may diminish due to increasing competition from other upward migrating tree species (Hiebert and Hamrick, 1984).

Communities are stable over a range of environmental conditions, but can rapidly change toward a new steady state if threshold conditions are exceeded (Gosz, 1992). Ecosystem stability is increased by the presence of many functional groups (Naeem *et al.*, 1999). The richness of the functional groups that we identified did not vary across forest types. Having several species within a functional group can be important for the resilience of that community as environmental conditions change (Walker, 1995; Naeem, 1998; Walker *et al.*, 1999). N-fixing plants in ponderosa pine forest are species rich, which could help preserve the functioning of the community as climate changes. Only two leguminous taxa, *Lathyrus lanszwertii* var. *leucanthus* and *Lathyrus* or *Vicia* spp., were found in all other forest types on the San Francisco Peaks. Since these two species are common in all forest types, they appear to have broad ecological tolerances (Table 3.1). If these species encounter problems migrating under changing climate, however, the missing functional group could result in ecosystem failure (Naeem, 1998).

Perry *et al.* (1990) suggested low abundance of AM fungi in coniferous forests could hinder migration of plants that associate chiefly with AM fungi. Our research showed AM inoculum is present in forests and should be available to facilitate species migrations. However, changes associated with climate change such as elevated CO₂, increasing temperatures, and decreased water availability may affect the colonization abilities of AM fungi (Monz *et al.*, 1994).

The indicator species that we identified may be valuable in monitoring changes throughout the San Francisco Peaks. Five indicator species were found in many forest types, but most reliably in one forest type, making them faithful but not exclusive indicators. They were *Elymus elymoides*, *Festuca arizonica*, *Lupinus* spp., and *Muhlenbergia montana* from ponderosa pine forest and *Pteridium aquilinum* from mixed conifer forest. Species, such as these, whose habitat extends into ecotones might be better able to migrate under changing climatic conditions (Stohlgren *et al.*, 2000). The remaining indicator species are more limited to the forest type in which they are indicators, but are not reliably found on every example of that forest type. Since this later group of indicator species are restricted to one forest type, they could be useful in monitoring the health of specific Arizona forest types (Carignan and Villard, 2002). Several non-indicator species were common in multiple forest types and could be predisposed to being successful migrants (Malcolm *et al.*, 2002). *Arenaria lanuginosa* ssp. *saxosa*, *Lathyrus lanszwertii* var. *leucanthus*, *Poa fendleriana*, *Pseudocymopterus montanus*, and *Senecio eremophilus* were found in all five forest types and were found on more than 20 belts in three or more forest types. *Frasera speciosa*, *Maianthemum stellatum*, and *Penstemon barbatus* were found in all five forest types and were found on more than 10 belts in two or more forest types.

Table 3.1 Plot characteristics by forest type. Standard Errors are shown in parenthesis.

	Ponderosa pine	Mixed conifer	Aspen	Spruce/fir	Bristlecone pine
Elevation (m)	2595 (15)	2778 (25)	2875 (27)	3224 (31)	3308 (32)
Slope (%)	16.1 (1.6)	31.6 (2.7)	31.0 (2.2)	41.1 (3.0)	52.9 (2.0)
Tree canopy cover (%)	51.5 (3.4)	69.9 (2.8)	65.7 (2.9)	57.0 (4.8)	40.1 (4.6)
Species richness	32.6 (1.4)	26.0 (1.4)	24.5 (1.0)	25.8 (2.4)	28.7 (1.1)
Shannon's H' diversity index	1.6 (0.1)	1.7 (0.1)	1.8 (0.1)	1.5 (0.2)	1.7 (0.1)
Exotic species richness	1.9 (0.4)	0.6 (0.2)	1.0 (0.2)	0.7 (0.2)	1.0 (0.2)
Understory plant cover (%)	31.8 (5.6)	22.3 (2.9)	49.4 (3.8)	16.6 (4.6)	27.4 (3.5)
Non-plant LICH	3.6 (0.9)	2.6 (0.9)	2.8 (0.7)	8.6 (1.8)	5.33 (1.4)
cover (%) LITT	57.2 (4.9)	55.7 (2.5)	34.3 (3.4)	55.1 (4.2)	47.0 (3.8)
ROCK	3.1 (0.9)	5.4 (1.2)	2.8 (0.5)	8.2 (2.4)	8.3 (1.9)
SOIL	0.7 (0.3)	0.4 (0.1)	1.1 (0.2)	0.6 (0.3)	6.95 (2.6)
WOOD	3.1 (0.5)	6.8 (0.6)	8.4 (0.7)	7.2 (1.8)	4.2 (0.7)
AM infection (%)	23.6 (5.1)	20.7 (2.2)	23.0 (2.0)	15.3 (3.7)	28.4 (4.6)
Non-AM infection (%)	3.6 (1.0)	2.6 (0.6)	2.0 (0.5)	0.7 (0.3)	3.92 (1.2)
10 most common species	<i>Carex</i> spp.	<i>Carex</i> spp.	<i>Lathyrus/Vicia</i> spp.	<i>Lathyrus lanszwertii</i>	<i>Carex</i> spp.
	<i>Festuca arizonica</i>	<i>Lathyrus lanszwertii</i>	<i>Carex</i> spp.	var. <i>leucanthus</i>	<i>Poa fendleriana</i>
	<i>Muhlenbergia montana</i>	var. <i>leucanthus</i>	<i>Lathyrus lanszwertii</i>	<i>Carex</i> spp.	<i>Arenaria lanuginosa</i>
		<i>Bromus</i> spp.	var. <i>leucanthus</i>	<i>Bromus</i> spp.	ssp. <i>saxosa</i>
	<i>Lathyrus/Vicia</i> spp.	<i>Pteridium aquilinum</i>	<i>Festuca arizonica</i>	<i>Lathyrus/Vicia</i> spp.	<i>Bromus</i> spp.
	<i>Elymus elymoides</i>	<i>Lathyrus/Vicia</i> spp.	<i>Bromus</i> spp.	<i>Mertensia franciscana</i>	<i>Lathyrus lanszwertii</i>
	<i>Poa fendleriana</i>	<i>Muhlenbergia montana</i>	<i>Muhlenbergia montana</i>	<i>Solidago</i> spp.	var. <i>leucanthus</i>
	<i>Cirsium</i> spp.			<i>Pseudocymopterus montanus</i>	<i>Solidago</i> spp.
	<i>Lupinus</i> spp.	<i>Poa fendleriana</i>	<i>Poa fendleriana</i>		<i>Muhlenbergia montana</i>
	<i>Pteridium aquilinum</i>	<i>Festuca arizonica</i>	<i>Pteridium aquilinum</i>	<i>Ribes montigenum</i>	<i>Hymenoxys hoopseii</i>
		<i>Elymus elymoides</i>	<i>Elymus elymoides</i>	<i>Hymenoxys hoopseii</i>	<i>Taraxacum officinale</i>
	<i>Ceanothus fendleri</i>	<i>Solidago</i> spp.	<i>Senecio eremophilus</i>	<i>Erigeron</i> spp.	<i>Festuca arizonica</i>

Table 3.2 Indicator species for each forest type. IV is the indicator value. A perfect indicator value would be 100.

Ponderosa Pine			Mixed Conifer			Aspen			Spruce/Fir			Bristlecone Pine		
Species	IV	p	Species	IV	p	Species	IV	p	Species	IV	p	Species	IV	p
<i>Cirsium</i> spp.	52.2	<0.01	<i>Thalictrum fendleri</i>	34.0	<0.01	No indicator species			<i>Pyrola</i> spp.	54.3	<0.01	<i>Festuca ovina</i>	48.1	<0.01
<i>Hieracium fendleri</i>	48.6	<0.01	<i>Pteridium aquilinum</i>	32.0	<0.01				<i>Aquilegia</i> spp.	25.2	<0.01	<i>Mertensia franciscana</i>	40.5	<0.01
<i>Packera multilobata</i>	48.4	<0.01	<i>Holodiscus dumosus</i>	31.1	<0.01							<i>Monardella glauca</i>	38.1	<0.01
<i>Astragalus rusbyi</i>	36.5	<0.01	<i>Mahonia repens</i>	29.2	<0.01							<i>Penstemon whippleanus</i>	37.5	<0.01
<i>Lotus</i> spp.	34.8	<0.01										<i>Hymenoxys hoopseii</i>	35.3	<0.01
<i>Oxytropis lambertii</i>	34.6	<0.01										<i>Potentilla</i> spp.	32.5	<0.01
<i>Ceanothus fendleri</i>	34.3	<0.01										<i>Ribes montigenum</i>	31.7	<0.01
<i>Verbascum thapsus</i>	32.6	<0.01										<i>Erigeron</i> spp.	26.8	0.01
<i>Antennaria parviflora</i>	30.9	<0.01												
<i>Elymus elymoides</i>	29.1	<0.01												
<i>Astragalus humistratus</i>	26.9	<0.01												
<i>Festuca arizonica</i>	26.9	<0.01												
<i>Lupinus</i> spp.	26.6	0.03												
<i>Muhlenbergia montana</i>	25.0	<0.01												

Table 3.3 Indicator species for plots with and without exotic species. IV is the indicator value. A perfect indicator value would be 100.

Plots with exotics			Plots with no exotics		
Species	IV	p	Species	IV	p
<i>Poa fendleriana</i>	52.8	<0.01	<i>Populus tremuloides</i>	46.9	<0.01
<i>Arenaria lanuginosa</i> ssp. <i>saxosa</i>	50.5	<0.01	<i>Pteridium aquilinum</i>	43.5	0.03
<i>Muhlenbergia montana</i>	50.3	0.03	<i>Mahonia repens</i>	39.6	<0.01
<i>Festuca arizonica</i>	48.7	0.05	<i>Pseudotsuga menziesii</i>	36.9	0.03
<i>Pseudocymopterus montanus</i>	41.8	0.01	<i>Thalictrum fendleri</i>	35.5	0.02
<i>Agoseris glauca</i>	36.9	<0.01	<i>Corallorrhiza maculata</i>	32.1	<0.01
<i>Achillea millefolium</i>	32.8	<0.01			
<i>Hymenoxys hoopesii</i>	29.5	<0.01			
<i>Potentilla</i> spp.	28.2	<0.01			

Table 3.4 Correlations with indicator species for plots with and without exotic species. No significant correlation is indicated by "ns."

	Species	Exotic Abundance		Exotic Richness		Native Abundance		Native richness	
		r	p	r	p	r	p	r	p
Plots with exotics	<i>Achillea millefolium</i>	0.54	<0.01	0.50	<0.01	0.47	<0.01	0.26	<0.01
	<i>Arenaria lanuginosa</i>	ns		ns		ns		0.24	0.01
	<i>ssp. saxosa</i>								
	<i>Festuca arizonica</i>	0.44	<0.01	0.51	<0.01	0.66	<0.01	0.28	<0.01
	<i>Muhlenbergia</i>	0.24	0.01	0.58	<0.01	0.38	<0.01	0.48	<0.01
	<i>montana</i>								
	<i>Poa fendleriana</i>	0.35	<0.01	0.46	<0.01	0.52	<0.01	0.38	<0.01
Plots without exotics	<i>Pseudocymopterus montanus</i>	0.60	<0.01	0.30	<0.01	0.49	<0.01	ns	
	<i>Mahonia repens</i>	ns		-0.23	0.01	ns		ns	
	<i>Populus tremuloides</i>	ns		ns		0.41	<0.01	ns	
	<i>Pteridium aquilinum</i>	0.26	<0.01	ns		ns		0.59	<0.01

Figure 3.1 Study sites on the San Francisco Peaks. Squares (■) show the permanent plots where we took soil samples. Dots (•) show the permanent plots where we did not take soil samples

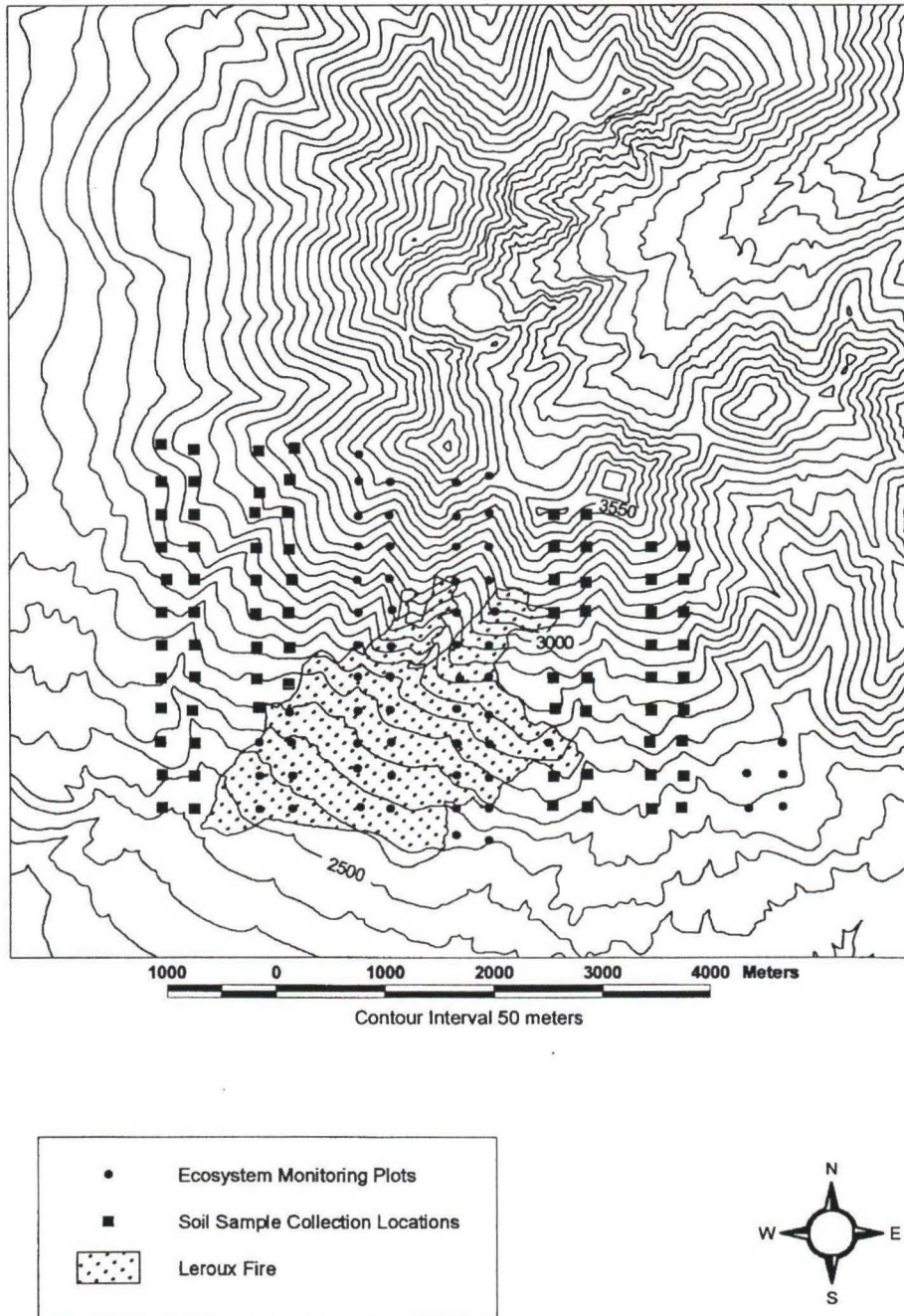


Figure 3.2 NMDS ordination comparing plots by forest type. Tree species were not included in this ordination. Ponderosa pine plots are indicated by stars (*), mixed conifer by open boxes (?), aspen plots by closed diamonds (?), spruce/fir by open circles (?), and bristlecone pine by closed triangles (?). The final result required 500 iterations to achieve final stress of 18.41 and final instability of 0.0048 ($p = 0.02$).

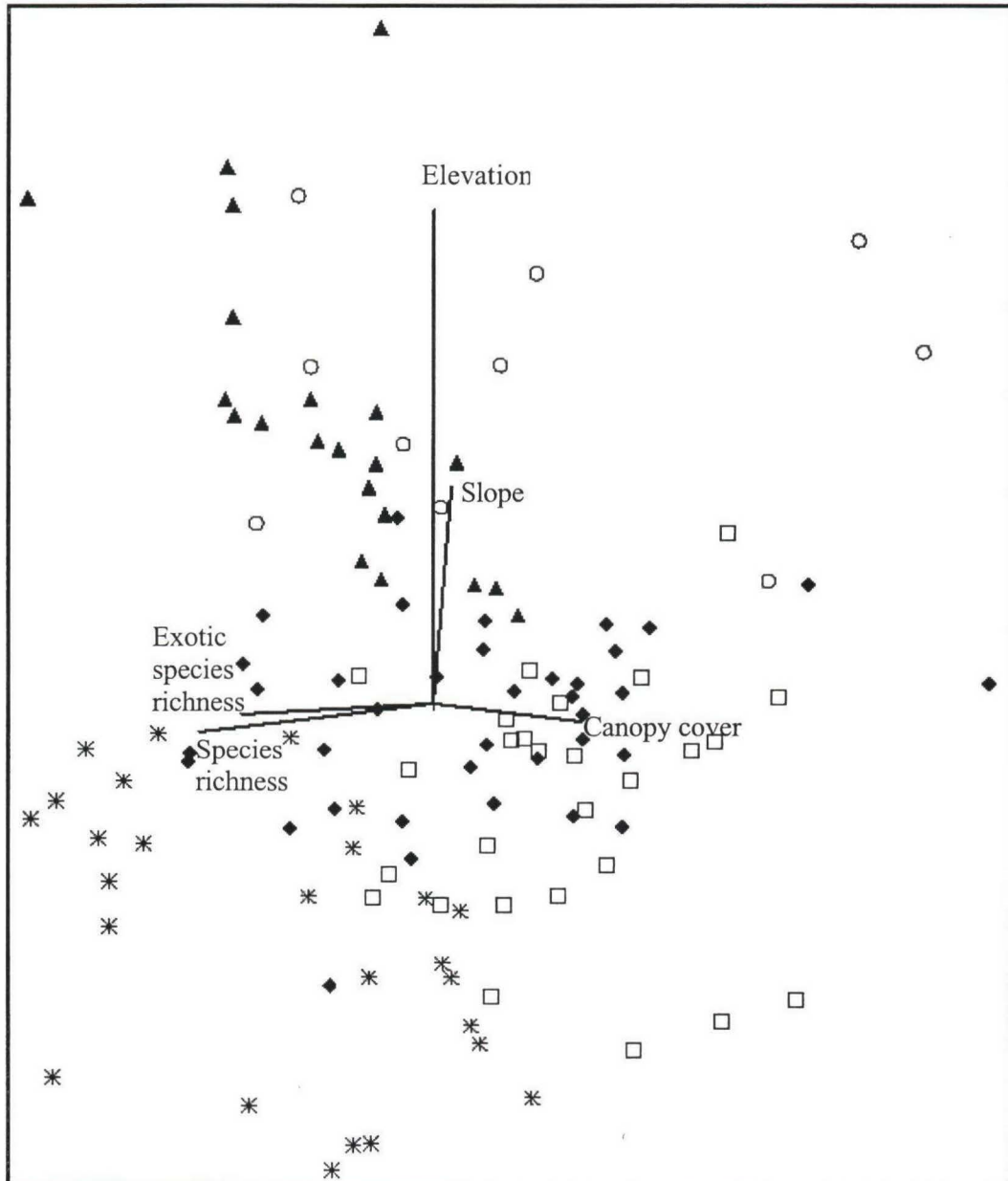


Figure 3.3 NMDS ordination comparing native species composition on plots with and without exotic species. Plots that had no exotic species are shown by the open circles (?). Plots where exotic species were present are shown by closed diamonds (?). The final result required 500 iterations to achieve final stress of 17.92 and final instability of 0.0048 ($p = 0.02$).

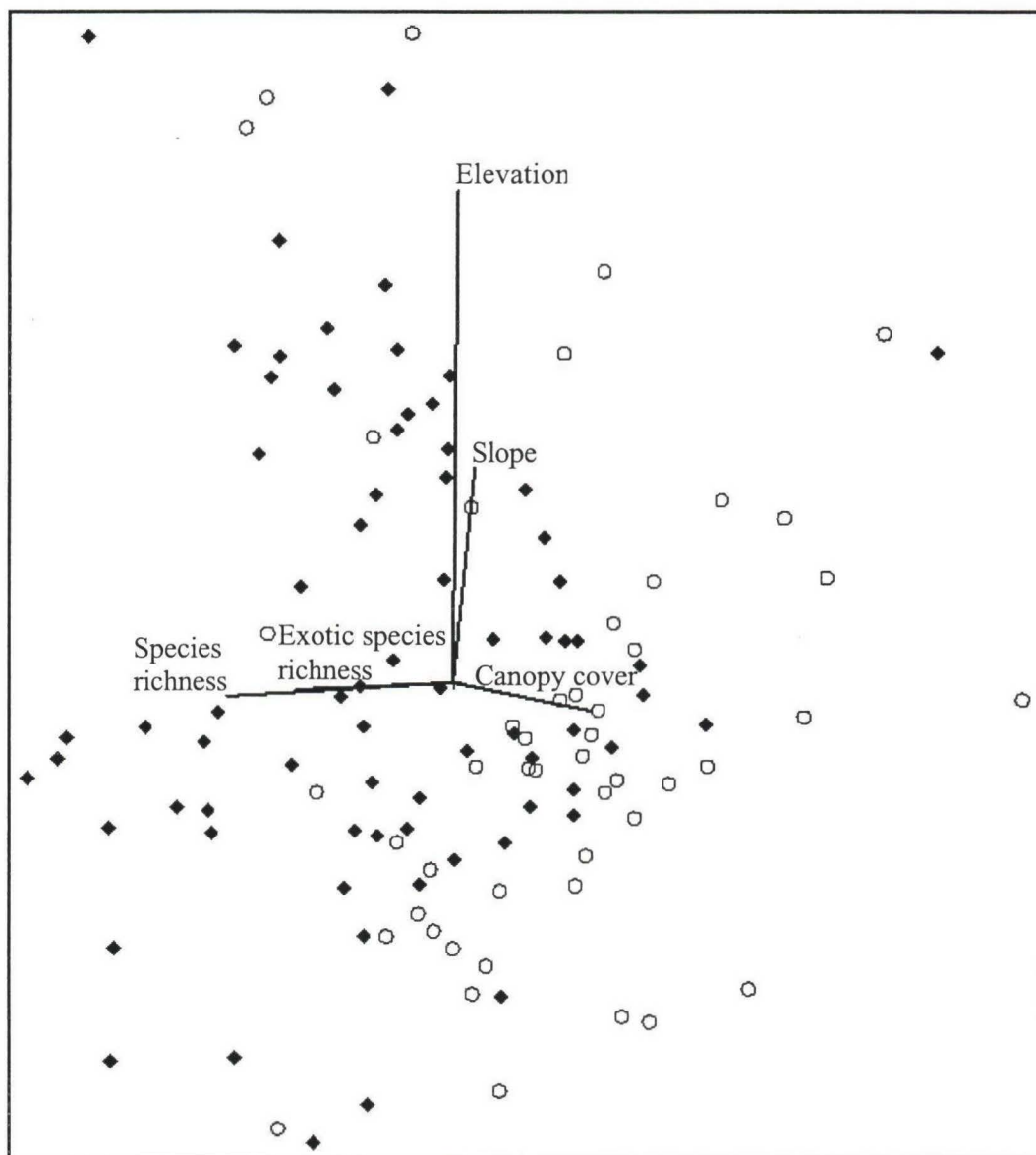
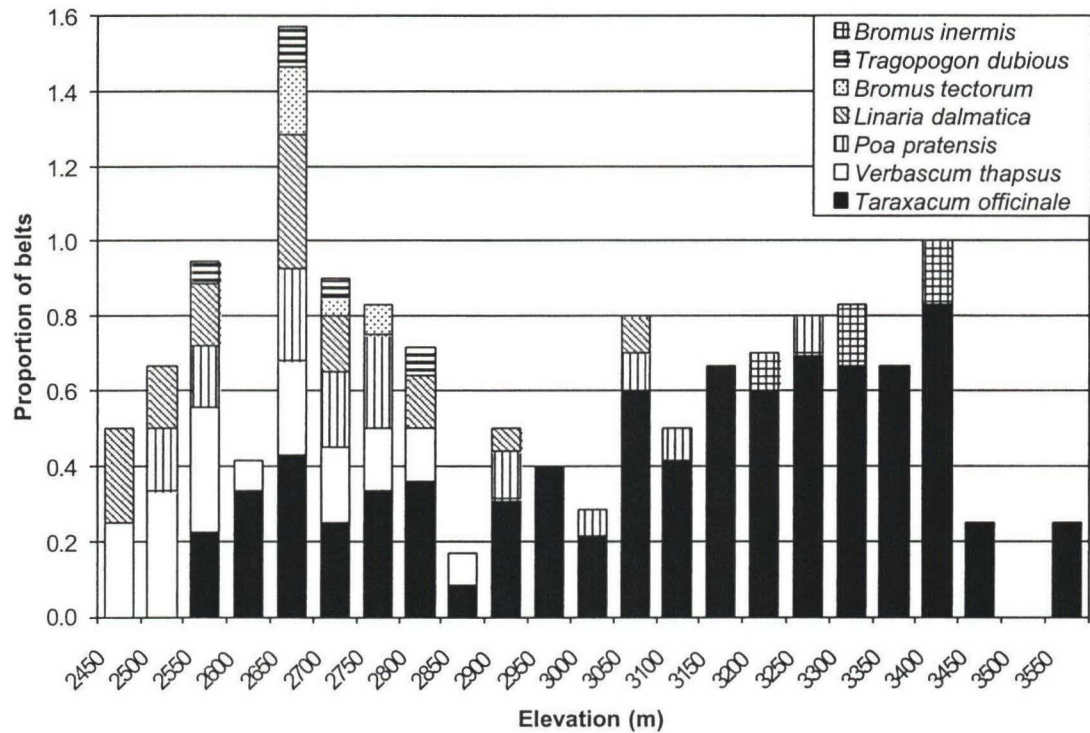


Figure 3.4 Proportion of belt plots with each exotic species. Only species which were found on > 1% of plots are shown.



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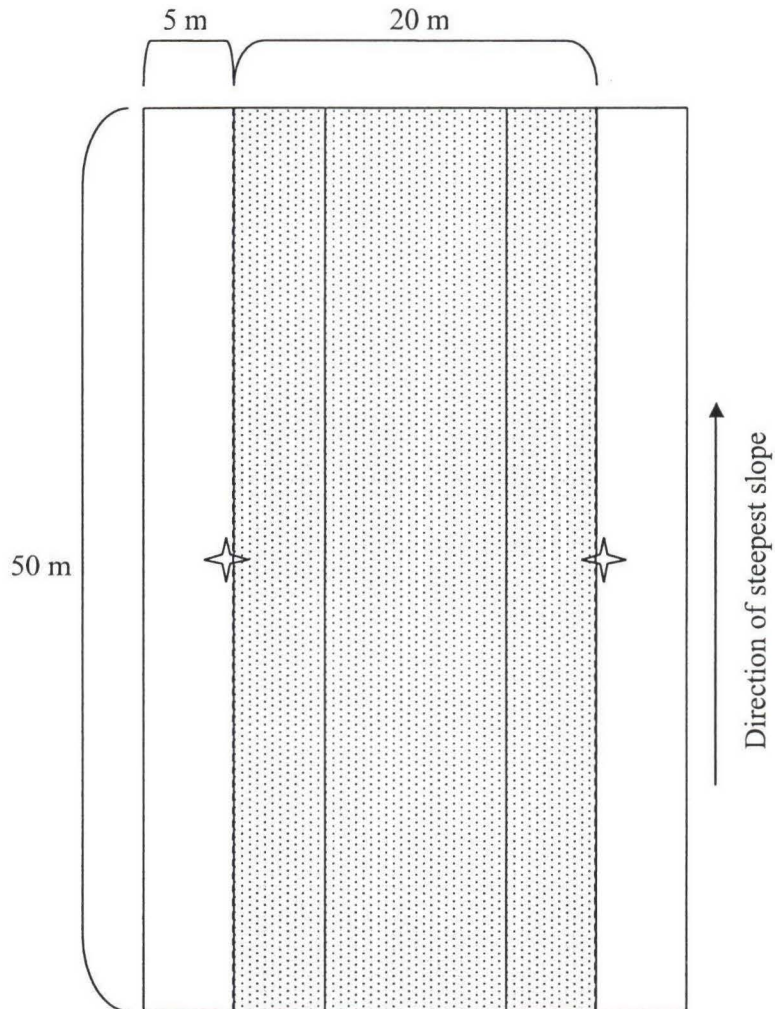
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APPENDIX 1: PLOT LAYOUT

The stippled area shows where I took overstory measurements. The dotted line is the point-lint intercept transect. The shaded area indicates the belt transect. I took two soil cores underneath the grass closest to the center of the belt, indicated by the star.



APPENDIX 2: CONSOLIDATION OF SPECIES

Changes made to species names in herbaceous data for the purpose of analysis.

Species for analysis	Species on datasheet	# Times	Reason
<i>Agastache</i> sp./	<i>Agastache pallidiflora</i>	2	Species very similar, easily mistaken for each other in field
<i>Dracocephalum</i> sp.	<i>Dracocephalum parviflorum</i>	21	
<i>Agoseris glauca</i>	<i>Agoseris</i> sp.	3	This was the only species found in study area
<i>Aquilegia</i> spp.	<i>Aquilegia caerulea</i>	2	Most <i>Aquilegia</i> were not flowering, and therefore indistinguishable
<i>Arabis</i> spp.	<i>Arabis fendleri</i>	9	These species most commonly seen as a basal rosette, making them indistinguishable from each other and other <i>Arabis</i> species
	<i>Pennellia longifolia</i>	9	
<i>Arenaria lanuginosa</i> ssp. <i>saxosa</i>	<i>Arenaria</i> sp.	8	Plots remeasured after the Leroux Fire had <i>A. lanuginosa</i> ssp. <i>saxosa</i> , all occurrences from early in study and unlikely to confuse <i>A. lanuginosa</i> and <i>A. fendleri</i>
<i>Astragalus humistratus</i> or <i>Astragalus rusbyi</i>	<i>Astragalus</i> spp.	6	Case by case basis, choose species found on same transect after Leroux Fire, if both species on belt transect, but only genus on Herb transect, used <i>Astragalus rusbyi</i> because it was more common
<i>Brickellia grandiflora</i>	<i>Brickellia</i> sp.	5	This was the only species found in study area
<i>Bromus</i> spp.	<i>Bromus anomalus</i>	8	Species very similar, easily mistaken for each other in field
	<i>Bromus ciliatus</i>	555	
<i>Carex</i> spp.	<i>Carex albonigra</i>	25	Species very similar, easily mistaken for each other in field
	<i>Carex deweyana</i>	41	
	<i>Carex duriuscula</i>	209	
	<i>Carex geophila</i>	253	
	<i>Carex occidentalis</i>	70	
	<i>Carex petasata</i>	2	
	<i>Carex rossii</i>	267	
<i>Castilleja</i> spp.	<i>Carex siccata</i>	694	Most <i>Castilleja</i> were not flowering, and therefore indistinguishable
	<i>Castilleja austromontana</i>	1	

Species for analysis	Species on datasheet	# Times	Reason
<i>Chenopodium</i> spp.	<i>Chenopodium album</i>	65	Species very similar, easily mistaken for each other in field
	<i>Chenopodium berlandieri</i>	15	
<i>Cirsium</i> spp.	<i>Cirsium wheeleri</i>	63	Many <i>Cirsium</i> spp. very similar, easily mistaken for each other in field
<i>Cystopteris</i> spp.	<i>Cystopteris fragilis</i>	2	Most <i>Cystopteris</i> were not flowering, and therefore indistinguishable
<i>Draba</i> spp.	<i>Draba asprella</i>	1	Most <i>Draba</i> were not flowering, and therefore indistinguishable
	<i>Draba aurea</i>	1	
	<i>Draba rectifruta</i>	1	
<i>Erigeron</i> spp.	<i>Erigeron formosissimus</i>	70	Species very similar, easily mistaken for each other in field
	<i>Erigeron speciosus</i>	48	
<i>Euphorbia</i> spp.	<i>Euphorbia brachycera</i>	28	Species very similar, easily mistaken for each other in field
	<i>Euphorbia incisa</i>	9	
<i>Frasera speciosa</i>	<i>Frasera</i> sp.	2	This was the only species found in study area
<i>Geranium</i> spp.	<i>Geranium caespitosum</i>	27	Most <i>Geranium</i> were not flowering, and therefore indistinguishable
	<i>Geranium richardsonii</i>	111	
<i>Holodiscus dumosus</i>	<i>Holodiscus</i> sp.	1	This was the only species found in study area
<i>Lathyrus</i> sp./ <i>Vicia</i> spp.	<i>Lathyrus graminifolius</i>	8	Species very similar, easily mistaken for each other in field
	<i>Vicia americana</i>	257	
	<i>Vicia pulchella</i>	4	
	<i>Vicia</i> spp.	14	
<i>Lithospermum multiflorum</i>	<i>Lithospermum</i> spp.	4	This was the only species found in study area
<i>Lotus</i> spp.	<i>Lotus utahensis</i>	1	Species very similar, easily mistaken for each other in field
	<i>Lotus wrightii</i>	15	
<i>Lupinus</i> spp.	<i>Lupinus argenteus</i>	415	Species very similar, easily mistaken for each other in field
	<i>Lupinus hillii</i>	49	
<i>Maianthemum stellatum</i>	<i>Maianthemum</i> sp.	7	This was the only species found in study area
<i>Mertensia franciscana</i>	<i>Mertensia</i> sp.	1	This was the only species found in study area
<i>Phlox gracilis</i>	<i>Phlox</i> sp.	1	This was the only species found in study area

Species for analysis	Species on datasheet	# Times	Reason
<i>Poa fendleriana</i>	<i>Poa</i> spp.	46	Most common <i>Poa</i> , frequently guessed as species in comments
<i>Potentilla</i> spp.	<i>Potentilla hippiana</i>	52	Did not realize <i>P. pulcherrima</i> , was on peaks until many were
	<i>Potentilla pulcherrima</i>	12	already mistakenly called <i>P. hippiana</i>
<i>Pyrola</i> spp.	<i>Orthilia secunda</i>	11	Species very similar, easily mistaken for each other in field
	<i>Pyrola chlorantha</i>	7	
	<i>Pyrola picta</i>	2	
	Pyrolaceae	1	
<i>Ribes montigenum</i> or <i>Ribes pinetorum</i>	<i>Ribes</i> spp.	17	Case by case basis based on guesses in comments or if one plant listed to species and one to genus, assumed both species present
<i>Rubus idaeus</i> ssp. <i>strigosus</i>	<i>Rubus</i> sp.	3	This was the only species found in study area
<i>Senecio wootonii</i>	<i>Senecio</i> spp.	2	Guess on datasheet
<i>Silene scouleri</i>	<i>Silene</i> sp.	1	This was the only species found in study area
<i>Solidago</i> spp.	<i>Oreochrysum parryi</i>	59	Species very similar, easily mistaken for each other in field
	<i>Solidago canadensis</i>	1	
<i>Symphoricarpos</i> <i>oreophilus</i>	<i>Symphoricarpos</i> sp.	4	This was the only species found in study area
<i>Trifolium longipes</i> ssp. <i>pygmaeum</i>	<i>Trifolium</i> sp.	2	This was the only species found in study area

APPENDIX 3: COMPLETE SPECIES LIST

Exotic species

Asteraceae

- Lactuca serriola* L.
Taraxacum officinale G.H.Weber ex Wiggers
Tragopogon dubius Scop.

Poaceae

- Bromus inermis* Leyss.
Bromus tectorum L. *Poa compressa* L.
Dactylis glomerata L. *Poa pratensis* L.

Rosaceae

- Sanguisorba minor* Scop.

Scrophulariaceae

- Linaria dalmatica* (L.) P. Mill
Verbascum thapsus L.

Native species

Apiaceae

- Perideridia parishii* (Coult. & Rose) A. Nels. & J.F. Macbr.
Pseudocymopterus montanus (Gray) Coult. & Rose

Apocynaceae

- Apocynum androsaemifolium* L.
Apocynum cannabinum L.

Asteraceae

- | | |
|--|--|
| <i>Achillea millefolium</i> L. | <i>Erigeron speciosus</i> (Lindl.) DC. |
| <i>Ageratina herbacea</i> (Gray) King & H.E. Robins. | <i>Heliomeris multiflora</i> Nutt. |
| <i>Agoseris glauca</i> (Pursh) Raf. | <i>Hieracium fendleri</i> Schultz-Bip. |
| <i>Antennaria marginata</i> Greene | <i>Hymenoxys hoopesii</i> (Gray) Bierner |
| <i>Antennaria parvifolia</i> Nutt. | <i>Hymenoxys richardsonii</i> var. <i>floribunda</i> (Gray) Parker |
| <i>Antennaria rosulata</i> Rydb. | <i>Laennecia schiedeana</i> (Less.) Nesom |
| <i>Artemisia campestris</i> L. | <i>Oreochrysum parryi</i> (Gray) Rydb. |
| <i>Artemisia carruthii</i> Wood ex Carruth. | <i>Packera franciscana</i> (Greene) W.A. Weber & A. Löve |
| <i>Artemisia dracunculus</i> L. | <i>Packera multilobata</i> (Torr. & Gray ex Gray) W.A. Weber & A. Love |
| <i>Artemisia ludoviciana</i> (Nutt.) Keck | <i>Pseudognaphalium macounii</i> (Greene) Kartesz |
| <i>Bahia dissecta</i> (Gray) Britt. | <i>Senecio actinella</i> Greene |
| <i>Brickellia grandiflora</i> (Hook.) Nutt. | <i>Senecio eremophilus</i> Richards |
| <i>Cirsium wheeleri</i> (Gray) Petrak | <i>Senecio wootonii</i> Greene |
| <i>Erigeron colomexicanus</i> A. Nels. | <i>Solidago</i> spp. L. |
| <i>Erigeron divergens</i> Torr. & Gray | <i>Solidago canadensis</i> L. |
| <i>Erigeron flagellaris</i> Gray | |
| <i>Erigeron formosissimus</i> Greene | |
| <i>Erigeron neomexicanus</i> Gray | |

Berberidaceae

- Mahonia repens* (Lindl.) G. Don

Boraginaceae

Cryptantha spp.

Lithospermum multiflorum Torr. ex
Gray

Macromeria viridiflora DC.

Mertensia franciscana Heller

Brassicaceae

Arabis spp. L.

Arabis fendleri Greene

Draba rectifracta C.L. Hitchc.

Draba spp. L.

Lepidium spp.

Draba asprella Greene

Pennellia longifolia (Benth.) Rollins

Draba aurea Vahl ex Hornem.

Thlaspi montanum L.

Caprifoliaceae

Lonicera arizonica Rehd.

Sambucus nigra L. ssp. *cerulea* (Raf.) R. Bolli

Symphoricarpos oreophilus Gray

Caryophyllaceae

Arenaria fendleri Gray

Arenaria lanuginosa ssp. *saxosa* (Gray) Maguire

Silene scouleri Hook.

Chenopodiaceae

Chenopodium spp. L.

Chenopodium album L.

Chenopodium berlandieri Moq.

Chenopodium leptophyllum (Moq.) Nutt. ex S. Wats.

Cupressaceae

Juniperus communis L.

Cyperaceae

Carex spp. L.

Carex albonigra Mackenzie

Carex occidentalis Bailey

Carex deweyana Schwein.

Carex petasata Dewey

Carex duriuscula C. A. Mey.

Carex rossii Boott

Carex geophila Mack.

Carex siccata Dewey

Dennstaedtiaceae

Pteridium aquilinum (L.) Kuhn

Dryopteridaceae

Cystopteris spp. Bernh.

Cystopteris fragilis (L.) Bernh.

Euphorbiaceae

Euphorbia brachycera Engelm.

Euphorbia incisa Engelm.

Fabaceae

- | | |
|--|--|
| <i>Astragalus humistratus</i> Gray | <i>Lupinus hillii</i> Greene |
| <i>Astragalus rusbyi</i> Greene | <i>Lupinus kingii</i> S. Wats. |
| <i>Lathyrus graminifolius</i> (S. Wats.) White | <i>Oxytropis lambertii</i> Pursh |
| <i>Lathyrus lanszwertii</i> var. <i>leucanthus</i> | <i>Thermopsis montana</i> var. <i>Montana</i> |
| (Rydb.) Dorn | Nutt. |
| <i>Lotus utahensis</i> Ottley | <i>Trifolium longipes</i> ssp. <i>pygmaeum</i> Nutt. |
| <i>Lotus wrightii</i> (Gray) Greene | <i>Vicia americana</i> Muhl. ex Willd. |
| <i>Lupinus argenteus</i> Pursh | <i>Vicia pulchella</i> Kunth |

Fumariaceae

- Corydalis aurea* Willd.

Gentianaceae

- Frasera speciosa* Dougl. ex Griseb.

Geraniaceae

- Geranium caespitosum* James
Geranium richardsonii Fisch. & Trautv.

Grossulariaceae

- Ribes montigenum* McClatchie
Ribes pinetorum Greene

Hydrophyllaceae

- Phacelia egena* (Greene ex Brand) Greene ex J.T. Howell

Iridaceae

- Iris missouriensis* Nutt.

Lamiaceae

- | | |
|--|---------------------------------|
| <i>Agastache pallidiflora</i> (Heller) Rydb. | <i>Monardella glauca</i> Greene |
| <i>Dracocephalum parviflorum</i> Nutt. | <i>Monarda pectinata</i> Nutt. |
| <i>Hedeoma drummondii</i> Benth. | |

Liliaceae

- | | |
|---|--|
| <i>Calochortus nuttallii</i> Torr. & Gray | <i>Maianthemum stellatum</i> (L.) Link |
| <i>Disporum trachycarpum</i> (S. Wats.) | <i>Zigadenus elegans</i> Pursh |
| Benth. & Hook. f. | <i>Linum lewisii</i> var. <i>lewisii</i> Pursh |

Monotropaceae

- Pterospora andromedea* Nutt.

Nyctaginaceae

- Mirabilis decipiens* (Standl.) Standl.

Onagraceae

- | | |
|-------------------------------------|---|
| <i>Chamerion angustifolium</i> ssp. | <i>Epilobium brachycarpum</i> K. Presl. |
| <i>circumvagum</i> (L.) Holub | <i>Gayophytum diffusum</i> Torr. & Gray |
| (Mosquin) Kartesz | <i>Oenothera</i> spp. L. |

Orchidaceae

- Corallorrhiza maculata* (Raf.) Raf.
Goodyera oblongifolia Raf.

Oxalidaceae

- Oxalis* spp. L.

Pinaceae

- | | |
|---|---------------------------------------|
| <i>Abies concolor</i> (Gordon & Glendinning) Lindl. | <i>Pinus aristata</i> Englem. |
| <i>Abies lasiocarpa</i> var. (Hook.) Nutt. var. <i>arizonica</i> (Merriam) Lemmon | <i>Pinus edulis</i> Engelm. |
| <i>Picea engelmannii</i> Parry ex Engelm. | <i>Pinus flexilis</i> James |
| | <i>Pinus ponderosa</i> P. & C. Lawson |
| | <i>Pseudotsuga menziesii</i> (Mirb.) |

Poaceae

- | | |
|--|---|
| <i>Agropyron</i> spp. Gaertn. | |
| <i>Blepharoneuron tricholepis</i> (Torr.) Nash | <i>Muhlenbergia montana</i> (Nutt.) A.S. Hitchc. |
| <i>Bromus anomalus</i> Rupr. ex Forn. | <i>Muhlenbergia virescens</i> (Kunth) Kunth |
| <i>Bromus ciliatus</i> L. | <i>Muhlenbergia wrightii</i> Vasey ex Coult. |
| <i>Elymus elymoides</i> (Raf.) Swezey | <i>Pascopyrum smithii</i> (Rydb.) A. Love |
| <i>Elymus glaucus</i> Buckl. | <i>Phleum pratense</i> L. |
| <i>Elymus trachycaulus</i> ssp. <i>trachycaulus</i> (Link) Gould ex Shinnars | <i>Piptochaetium pringlei</i> (Beal) Parodi |
| <i>Festuca arizonica</i> Vasey | <i>Poa fendleriana</i> (Steud.) Vasey |
| <i>Festuca ovina</i> L. | <i>Poa nemoralis</i> ssp. <i>interior</i> L. (Rydb.) W.A. |
| <i>Hesperostipa comata</i> (Trin. & Rupr.) Barkworth | <i>Schizachyrium scoparium</i> (Michx.) Nash |
| <i>Koeleria macrantha</i> (Ledeb.) J.A. Schultes | <i>Trisetum spicatum</i> (L.) Richter |

Polemoniaceae

- Phlox* sp. L.
Polemonium pulcherrimum Hook.
Polemonium viscosum Nutt.

Polygonaceae

- Eriogonum racemosum* Nutt.
Oxyria digyna (L.) Hill
Polygonum douglasii Greene

Primulaceae

- Androsace septentrionalis* L.
Primula parryi Gray

Pyrolaceae

- | | |
|------------------------------------|------------------------------|
| <i>Orthilia secunda</i> (L.) House | <i>Pyrola chlorantha</i> Sw. |
| <i>Pyrola</i> spp. L. | <i>Pyrola picta</i> Sm. |

Ranunculaceae

- | | |
|---|--|
| <i>Actaea rubra</i> ssp. <i>arguta</i> (Nutt.) Hulten | |
| <i>Aquilegia</i> spp. L. | <i>Ranunculus inamoenus</i> Greene |
| <i>Aquilegia caerulea</i> James | <i>Thalictrum fendleri</i> Engelm. ex Gray |

Rhamnaceae

- Ceanothus fendleri* Gray

Rosaceae

- | | |
|--|---|
| <i>Amelanchier</i> sp. | <i>Potentilla hippiana</i> Lehm. |
| <i>Fragaria virginiana</i> Duchesne | <i>Potentilla pulcherrima</i> Lehm. |
| <i>Geum rossii</i> var. <i>turbinatum</i> (R. Br.)
Ser. Var | <i>Potentilla subviscosa</i> Greene |
| <i>Geum triflorum</i> Pursh | <i>Rosa woodsii</i> Lindl. |
| <i>Holodiscus dumosus</i> (Nutt. ex Hook)
Heller | <i>Rubus idaeus</i> ssp. <i>strigosus</i> (Michx.)
Focke |
| <i>Potentilla crinita</i> Gray | <i>Sorbus dumosa</i> Greene |

Rubiaceae

- Houstonia wrightii* Gray
Kelloggia galioides Torr.

Salicaceae

- Populus tremuloides* Michx.
Salix scouleriana Barrat ex. Hook

Saxifragaceae

- Heuchera rubescens* Torr.

Scrophulariaceae

- | | |
|---|---------------------------------------|
| <i>Besseyia arizonica</i> Pennell | <i>Penstemon barbatus</i> (Cav.) Roth |
| <i>Castilleja</i> spp. Mutis ex L. f. | <i>Penstemon rostriflorus</i> Kellogg |
| <i>Castilleja austromontana</i> Standl. &
Blumer | <i>Penstemon virgatus</i> Gray |
| | <i>Penstemon whippleanus</i> Gray |

Solanaceae

- Nicotiana attenuata* Torr. ex S. Wats.

Violaceae

- Viola canadensis* L.

Viscaceae

- Arceuthobium* sp. Bieb.

Unknown origin

Asteraceae

- Cirsium* spp. P. Mill.

Brassicaceae

- Descurainia* sp. Webb & Berth.

SPECIES AND CANOPY COVER MAP DEVELOPMENT USING LANDSAT ENHANCED THEMATIC MAPPER IMAGERY FOR GRAND CANYON NATIONAL PARK

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ABSTRACT

Overstory vegetation maps of species and canopy cover were developed from Landsat 7 Thematic Enhanced Thematic Mapper satellite imagery. Ecosystem Monitoring plot data, collected during the 1997-2001 field seasons, were used as training sites for the image classification. Sixty-two species classes and four canopy cover classes were mapped. The maps will be used to support a Joint Fire Science Program funded project to model long-term fire regimes and ecological change using fire history, climate, and forest structure data. The calibrated model will then be used to assess fire behavior under current fuel conditions and to evaluate and compare future fuel treatments that may include prescribed burning and thinning.

INTRODUCTION

We developed landscape-scale information on forest species composition (vegetation type) and canopy characteristics in support of a larger study on ecological changes in forest structure and fire regime. In most southwestern forests, fire ecology research has focused on ponderosa pine and lower mixed conifer forests, where well-preserved fire scars are used to reconstruct detailed histories of surface fire. This method stands in contrast to the research approach usually applied in boreal forests, where maps of forest stands that originated after stand-replacing fires form the base data for reconstructing fire history. In this study, we had the opportunity to combine both methods to reconstruct changes over an elevational gradient from ponderosa pine forest, with a surface fire regime, to spruce-fir and aspen forests, with a mixed fire regime that included stand-replacing burns. Remotely sensed data, combined with extensive systematic ground sampling, were necessary for creating the large-scale coverages for analysis.

Fire regime characteristics of high-elevation forests on the North Rim of the Grand Canyon, Arizona, were reconstructed from fire scar analysis, remote sensing, tree age, and forest structure measurements (Fulé et al, 2002 and in review). Analysis of fire scar samples indicates that surface fires were common from 1700 to 1879 in the 4,400 ha site, especially on S and W aspects. Fire ignition point data for a portion of the study area, collected by the National Park Service between 1924 and 1996 (Figure 1), shows that fires, both lightning and human caused, are quite frequent. Fire dates frequently coincided with fire dates measured at study sites at lower elevation, suggesting that pre-1880 fire sizes may have exceeded 50,000 ha. Currently the forest is predominantly spruce-fir, mixed conifer, and aspen. In contrast, dendroecological reconstruction of past forest structure showed that the forest in 1880 was very open, corresponding closely with historical (Lang and Stewart 1910) accounts of severe fires leaving partially denuded landscapes. Severe fires were not unprecedented in the pre-1880 forest, but the exclusion of frequent surface fires in the mixed conifer and ponderosa pine forests has led to a more homogenous landscape where the extent and severity of contemporary fires may exceed pre-1880 patterns.

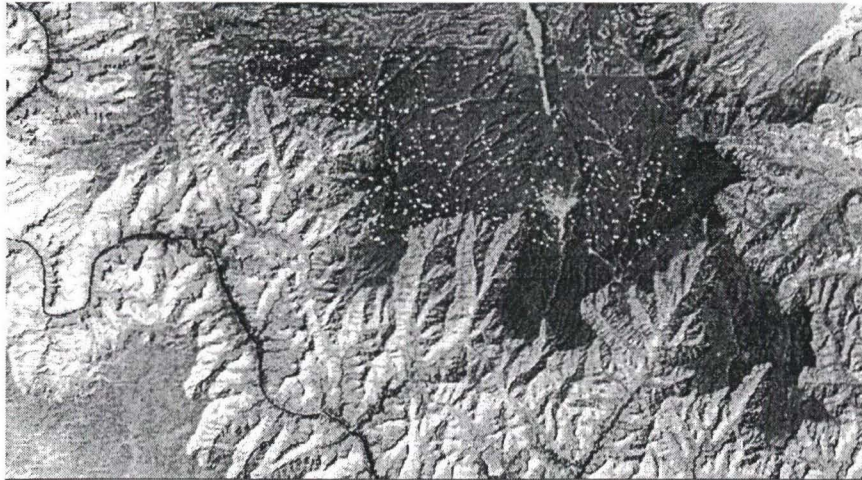


Figure 1; Fire ignition points

METHODS

Study Area

The study site (Figure 2) was a portion of the South Rim, a section of the Canyon itself, and the entire North Rim area located within the National Park. A portion of the North Kaibab National Forest, just north of the Park boundary, was also included. The main focus of this project was the North Rim portion of the study area. This portion of the site completed a transect of study sites described by Fulé et al. (2002). The lower transect ranged from Powell Plateau, Fire Point, and Rainbow Plateau, each ~2,300 m elevation, through Swamp Ridge (~2,500 m). While the complete transect ran west-east along the northern border of Grand Canyon National Park, the prevailing fire season winds are from the southwest. Therefore we added a new study site, Galahad Point, at the base of Kanabowits Canyon (~2,350 m elevation). The Galahad site lay directly downcanyon and upwind from Little Park, allowing us to test whether fire dates differed among low-elevation sites southwest vs. due west of the high-elevation site.

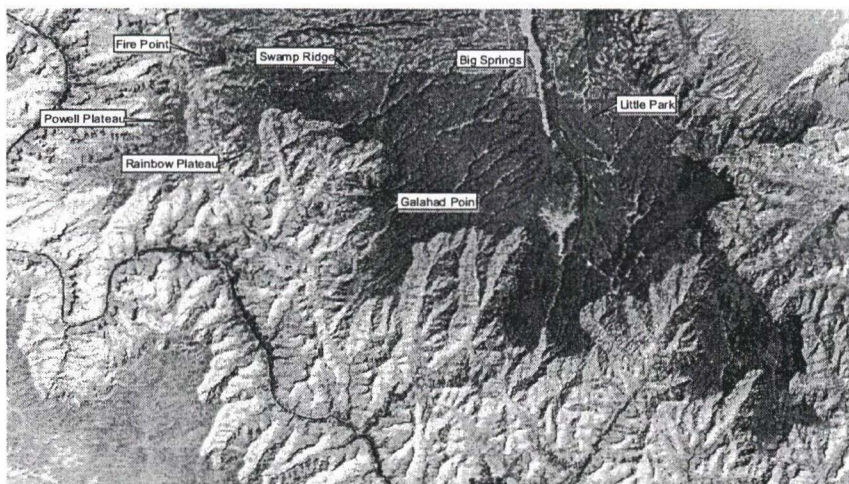


Figure 2; Study site

The average January temperature is -2° C and the average July temperature is 17° C. Precipitation occurs during the winter months, in the form of snow, and during the summer monsoonal season. Average precipitation is 64 cm and the average snowfall is 318 cm (Warren et al. 1982).

Forests in the lower elevation areas of the study site, such as Galahad Point and Powell Plateau, were dominated by ponderosa pine with Gambel oak (*Quercus gambelii*) and New Mexican locust (*Robinia neomexicana*). At Little Park and Big Springs, tree species included ponderosa pine (*Pinus ponderosa*), aspen (*Populus tremuloides*), white fir (*Abies concolor*), and subalpine fir (*Abies lasiocarpa*). Two spruce species were encountered: Engelmann (*Picea engelmannii*) and blue spruce (*Picea pungens*). Both species were combined as "spruce" in this study because of difficulties in distinguishing young trees (Moore and Huffman in review) and our observation of trees at the study site that had characteristics intermediate between the two species.

Dataset

For this project, a Landsat 7 Enhanced Thematic Mapper (ETM) image, acquired 6 June 2000, was used. TM imagery has been shown to be the best product for consistently mapping vegetation for large land areas (Keane et al. 2000). Landsat Thematic Mapper imagery has been used extensively for vegetation mapping projects (Golden 1991, Congalton et al. 1993, Muldavin et al. 1998, Vanderzanden et al. 1999, Keane et al. 2000).

The aerial photography for the study area is National High Altitude Photography program (NHAP) 1:40,000 color infrared prints. A digital elevation model (DEM), with 30 m spatial resolution, was used as a tool to refine the vegetation classification.

Preprocessing

The project area, with a buffer, was clipped from the ETM imagery to reduce processing time and storage space. A ratio band of band 3 (visible red) with band 4 (near infra-red) was created and added to the original six reflective bands. This particular ratio has proven to be useful for minimizing shadow effects in satellite image classifications (Vanderzanden et al. 1999). The Texture module in Imagine was used to create a texture file using band 4. This band was added to the ETM dataset.

An unsupervised classification with 75 classes was run to identify non-forest and below rim areas. The DEM was used to separate below rim areas that were confused with above rim areas. No large water bodies or developed areas exist in the project area that needed to be masked from the imagery. The non-forest classes were given the appropriate labels (grass, grass-shrub, etc.) and masked from the imagery. They were not included in the remainder of the processing. This was done to reduce the spectral variation within the image.

Training Site Selection

Training sites are areas on the ground used to represent a particular cover type or structural stage category (Lachowski et al., 1995). The Ecosystem Monitoring (EM) plot data collected in the 1997-2001 field seasons was used as training sites for the classification process. The EM plot centers are 300 m apart and are a subset from a plot grid that covers the entire study area. A total of 202 20 x 50 m plots were established and 188 were used as training sites (Figure 3).

These plots were not established with the intention of being utilized as training sites for image classification but the data collected for each plot does make them well suited for this purpose. Overstory tree data collected includes species, dbh, dsh for a subset of the trees, and tree height. Tree canopy cover, as well as understory vegetation data, are collected on the two 50 m plot edges and fuels data are collected on four 25 m transects that originate from the centerline (long axis) of the plot. Understory tree data are collected for ¼ of the plot. Slope and aspect are recorded for all plots. Plot elevations were taken from the DEM.

All image classification and analysis was done using Erdas Imagine. The training sites were digitized directly on the ETM imagery to create a supervised training site signature file. Each training site polygon included at least 10

pixels including the pixel or pixels that corresponded with each EM plot center. Each training site was given a species classification label after it was digitized.

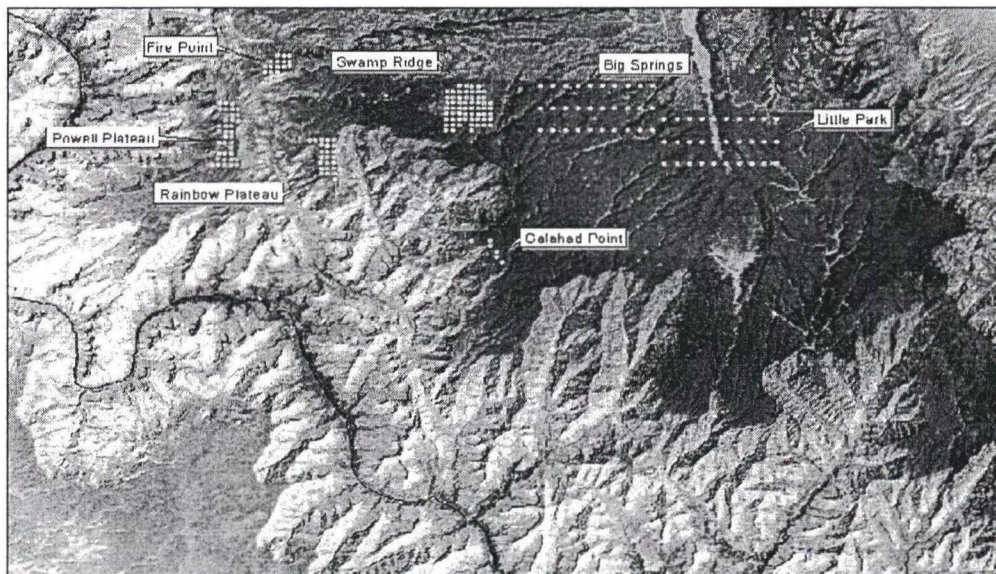


Figure 2; Training site locations

Classification scheme

The classification scheme for this project was developed so that it would fit within the National Vegetation Classification Standards (NVCS) framework. The NVCS has been developed through the USGS-NPS Vegetation Mapping Program in association with USGS/BRD, EPA, National Park Service, The Nature Conservancy, Ecological Society of America, and others (USGS, 2000). The goal of the NVCS is to provide a consistent national vegetation classification system

The EM plot data were analyzed to determine the species labels that were assigned to each of the training sites. The species label for each training site was based on 'importance value' (Taylor 2000) calculated as the sum of the relative frequency (percent stems) and relative abundance (percent basal area) for each species. The labels were arranged to reflect the dominant species for each training site. A total of fifty-three species classes were created using the described method. Nine additional classes were added to account for the below rim vegetation and the burned area from the 2001 Outlet Fire. These sixty-two classes were collapsed into ten classes (Table 1) to facilitate the analysis.

Mixed Conifer
 Spruce-fir
 Ponderosa Pine
 Aspen
 Gambel Oak
 Pinyon-Juniper
 Burn
 Mohave Desert
 Scrub
 Meadow
 Grass-Shrub

Table 1; Species and landcover classes

Spectral Analysis

The unsupervised and supervised training site signature files were combined and input into a statistical software package and clustered. Clusters that included two or more supervised signatures with similar labels were retained. Clusters that included a supervised signature and an unsupervised signature were also retained. Supervised signatures, with dissimilar labels, that clustered together, indicated that one or both of the signatures needed to be reevaluated. Spectral confusion between signatures may be due to topographic effects, mislabeling of one or both of the signatures, or a placement error made during the digitizing process. It is also possible that the signatures may not be statistically separable. Erdas Imagine has programs that were used to determine signature separability. Two or more unsupervised signatures that clustered together indicated areas within the study area whose spectral parameters were not captured with the supervised training sites. This may be due to an actual vegetation variable that was not sampled in the field or it may be due to topographic effects. These polygons were then digitized onto the imagery. The final set of signatures from this spectral analysis process were used for image classification.

Supervised Classification and Editing

A classification using a minimum distance algorithm was run using the combined training site signature set. The classified image was checked using the aerial photographs. Individuals familiar with the area assisted in reviewing and refining the classification. Any signatures that were consistently classifying correctly were masked from the image and not used for further processing. Signatures that consistently misclassified the image were evaluated to determine if they had to be removed from the signature set. Training sites were sometimes redigitized in an attempt to improve the classification. They were also sometimes relabeled to reflect the cover type that they were classifying.

A model was developed in Imagine, using the DEM, to assist in the identification of misclassified pixels. Vegetation types such as Gambel Oak and New Mexico Locust do not occur at the higher elevations of the study area. The model "flagged" these vegetation types if they occurred above 2250 m. These pixels were then edited to reflect the correct vegetation type. Mixed conifer pixels below 2200 m were also identified and edited.

Canopy cover was mapped, into four forested classes and four non-forested classes (Table 2), using training sites that were photo-interpreted from the 1:40,000 aerial photography. During the supervised classification process, training sites were added as needed to refine the classification. A total of fifty-eight training sites were used to develop the supervised classification.

11-25%
26-40%
41-70%
71-100%
Below Rim Vegetation
Burn
Meadow
Grass/Shrub

Table 2; Canopy cover class

Results and future work

Table 3 shows the areas and relative areas for the ten species and landcover types. Pinyon-juniper was the most common type because of the large amount of below rim vegetation within the mapped area. Ponderosa pine, mixed conifer, and spruce-fir are the most common vegetation types on the North Rim.

Cover Type	Area (ha)	Percent of Area	Fuel Model
Mixed Conifer	5,375	3.5%	8
Spruce-fir	2,450	1.6%	10
Ponderosa Pine	35,892	23.4%	9
Aspen	3,820	2.5%	8
Gambel Oak	3,810	2.5%	9
Pinyon-Juniper	94,920	61.8%	6
Burn	3,033	2.0%	11
Mohave Desert			
Scrub	2,100	1.4%	5
Meadow	880	0.6%	1
Grass-Shrub	1,250	0.8%	2
total	153,530		

Table 3; Total area, relative area, and Anderson fuel model type of the species and landcover types

Plans for future work include using the data layers as inputs to fire behavior simulation models. The species coverage has already been recoded to their corresponding Anderson (1982) fuel models. The models will be used to evaluate alternative future fuel treatments.

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